

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LES MÉCANISMES D'INVASION DE LA COCCINELLE
ASIATIQUE *HARMONIA AXYRIDIS* PALLAS AU QUÉBEC

THÈSE

PRÉSENTÉE COMME EXIGENCE PARTIELLE
DU DOCTORAT EN BIOLOGIE

PAR

GENEVIÈVE LABRIE

AVRIL 2007

UNIVERSITÉ DU QUÉBEC À MONTRÉAL
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REMERCIEMENTS

Une thèse de doctorat, malgré ce qu'on en dit, ne se fait pas seul dans un coin. Beaucoup de gens sont impliqués dans cette œuvre. Je ne serais pas passée au travers de cette aventure sans l'appui et les encouragements de nombreuses personnes. Je vais tenter, par ces quelques mots, de leur exprimer toute ma gratitude et ma reconnaissance.

La réalisation de ce doctorat n'aurait pas eu lieu sans la confiance et la compréhension de mon directeur de recherche Daniel Coderre. Lors de nos discussions, tant professionnelles que personnelles, il a toujours su trouver les mots d'encouragement qui illuminaient le reste de la journée et qui me motivaient à continuer la recherche.

Cette thèse a été pour moi une source continue de réflexion grâce aux nombreuses discussions avec mon co-directeur Éric Lucas. Je veux lui exprimer ma profonde reconnaissance pour son appui constant, sa grande compréhension ainsi que ses encouragements, qui m'ont permis de faire progresser et de terminer cette thèse.

Je remercie chaleureusement aussi toutes les personnes qui ont participé aux différents comités d'encadrement de ce doctorat, soit William Vickery, Luc-Alain Giraldeau et Paul del Giorgio.

Ce projet a été rendu possible grâce à une bourse d'étude et une subvention de recherche du Conseil de Recherche en Sciences Naturelles et en Génie du Canada, que je remercie grandement.

Il est indispensable d'exprimer ma reconnaissance aux assistants (es) de terrain qui m'ont permis de mener à bien les différentes expériences effectuées durant cette thèse. Je remercie grandement Raphaël Dubé, Annie-Ève Gagnon-Thibodeau, Isabelle Desjardins et Fanie Courchesne pour leur joie de vivre, leurs compétences et leur organisation qui ont su rendre la prise de données efficace et agréable. Il me fait

plaisir aussi de remercier chaleureusement tous les membres du laboratoire de lutte biologique qui ont su apporter de longues discussions professionnelles, personnelles et beaucoup de plaisir à venir travailler grâce à l'ambiance chaleureuse qu'ils ont su créer : Isabelle Gagné, Franz Vanoosthuyse, Caroline Provost, Benoit Guénard, Samuel Pinna, Olivier Aubry, Louise Voynault, Nathalie Roullé, Jacinthe Tremblay, Claudio Nunes, Julie Bourgeault, Bruno Fréchette, Jennifer de Almeida, Hugo Trottier, Arnaud Santis ainsi que Mircea Bejan. Je voudrais aussi remercier Nicolas Legault, du labo d'à côté, qui était là pour aller prendre un café et placoter!

Je voudrais remercier ma famille, particulièrement mes parents, Michel Labrie et Nicole Naud, qui m'ont transmis leur amour de la nature et de la recherche de connaissances, mais aussi pour l'intérêt qu'ils ont porté à ma recherche. Je voudrais aussi souligner l'appui de mes sœurs, Katherine et Caroline, tout au long de mon doctorat.

Finalement, je voudrais remercier du fond du cœur mon conjoint Janick Durocher, pour tout l'amour et les encouragements qu'il m'a apportés tout au long de ce projet. Merci d'avoir été le pilier sur lequel je me suis appuyée dans les moments plus difficiles. Je remercie aussi mes deux enfants, Élie et Colin, pour leur sourire, leur joie de vivre et leur curiosité insatiable qui m'ont procuré l'énergie nécessaire à la réalisation de ce projet.

AVANT-PROPOS

Les quatre chapitres de cette thèse ont été publiés, soumis ou sont en préparation pour différentes revues scientifiques. Bien que certains collaborateurs apparaissent comme co-auteurs des chapitres, l'auteure de cette thèse fut entièrement responsable de l'élaboration des protocoles expérimentaux, de la réalisation des expériences, de l'analyse de données et de la rédaction de l'ensemble de cette thèse.

Chapitre I : Can developmental and behavioral characteristics of the multicoloured Asian lady beetle *Harmonia axyridis* explain its invasive success? *Biological Invasions* 8 : 743-754.

Geneviève Labrie, Éric Lucas et Daniel Coderre

Chapitre II : May competitive abilities of *Harmonia axyridis* explain its invasive success? *Entomologia Experimentalis et Applicata* (En préparation).

Geneviève Labrie, Nicolas Legault, Daniel Coderre et Éric Lucas

Chapitre III: Overwintering strategy of the multicolored Asian lady beetle (Coleoptera: Coccinellidae): cold-free space as a factor of invasive success. *Annals of the Entomological Society of America* (2007, accepté).

Geneviève Labrie, Daniel Coderre et Éric Lucas

Chapitre IV: Is invasive success of the multicolored Asian ladybeetle *Harmonia axyridis* influenced by resource productivity? (En préparation).

Geneviève Labrie, Daniel Coderre et Éric Lucas

Deux autres publications, pour lesquelles j'ai participé de façon active à la prise de données et à la rédaction, sont incluses dans la thèse en annexe, qui ajoutent des informations supplémentaires sur la capacité d'invasion de la coccinelle asiatique ainsi que sur ses impacts.

Annexe A : Are annual crops more prone to invasive species than perennial crops ?
The case of the multicolored Asian ladybeetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). (En préparation)

Éric Lucas, Charles Vincent, Geneviève Labrie, Gérald Chouinard, François Fournier, Francine Pelletier, Noubar J. Bostanian, Daniel Coderre, Marie-Pierre Mignault et Pierre Lafontaine.

Annexe B: The Multicoloured Asian Lady beetle, *Harmonia axyridis* - beneficial or nuisance organism? *Dans* Vincent, C., M. Goettel et G. Lazarovitz (eds.) Case studies in biological control : a global perspective. CABI Publishing, UK. (2007, sous presse)

Éric Lucas, Geneviève Labrie, Charles Vincent et Joseph Kovach

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RÉSUMÉ

Les invasions biologiques représentent maintenant une cause majeure du changement global de la planète. Les pertes économiques et environnementales de ces invasions sont de l'ordre de milliard de dollars chaque année. Afin de prévenir, prédire et contrôler ces invasions, il est indispensable de mieux comprendre les caractéristiques biologiques et traits d'histoire de vie de ces espèces, leurs interactions avec les communautés natives et l'influence de l'environnement sur leur succès d'invasion. Au Québec, nous faisons face depuis quelques années à l'invasion de la coccinelle asiatique *Harmonia axyridis* Pallas, introduite à plusieurs reprises en Amérique du Nord à des fins de lutte biologique au cours du siècle précédent. L'objectif principal de ce projet de doctorat était de déterminer les mécanismes régissant l'invasion de *H. axyridis* au Québec en examinant plus attentivement certaines caractéristiques de l'espèce, telles son développement et ses comportements d'alimentation, ses interactions au sein de la communauté aphidiphage et l'influence de deux caractéristiques environnementales, la température hivernale et la productivité du milieu, sur la survie et la croissance de population de cette espèce envahissante. Les différents aspects de l'espèce, de la communauté et de l'environnement ont été comparés entre la coccinelle asiatique et une espèce de coccinelle indigène, la coccinelle maculée (*Coleomegilla maculata lengi* Timberlake).

Les résultats ont révélé que la coccinelle asiatique se développait plus rapidement durant le 2^{ème} stade larvaire et qu'elle atteignait le 4^{ème} stade larvaire plus rapidement que la coccinelle maculée. Un 5^{ème} stade larvaire a été découvert chez la coccinelle asiatique, où les individus présentaient un temps de développement total similaire aux autres individus, mais avec une voracité accrue et un gain de poids plus élevé, suggérant une meilleure valeur adaptative pour ces individus. Ces caractéristiques du développement de la coccinelle asiatique, ajoutées à son efficacité de prédation et aux caractéristiques comportementales permettraient à cette espèce une croissance plus efficace et des habiletés prédatrices accrues et pourraient contribuer à sa capacité d'invasion.

Les interactions entre la coccinelle asiatique, la coccinelle maculée et la coccinelle à 14 points *Propylea quatuordecimpunctata* L., ont démontré que la coccinelle asiatique était un prédateur intragilde plus efficace que les deux autres espèces. Aucune prédation n'a été effectuée par la coccinelle maculée et la coccinelle à 14 points sur les larves de 4^{ème} stade et les pupes de la coccinelle asiatique, ce qui pourrait lui procurer un avantage certain lors de son invasion. Toutefois, la coccinelle asiatique est tout de même vulnérable à la prédation, car les œufs et les jeunes stades larvaires étaient consommés par les deux autres espèces. Aucun effet indirect ou direct des interactions n'a été mesuré sur la perte de poids et la survie de la coccinelle asiatique et de la coccinelle maculée dans une expérience sur plants de gourgane. Les capacités de prédation de la coccinelle asiatique au sein des communautés aphidiphages pourraient toutefois expliquer son succès d'invasion lorsque celle-ci est de plus grosse taille que ses protagonistes.

La coccinelle asiatique n'a pas survécu à l'extérieur durant l'hiver 2003-2004 sur les sites d'hibernation de la coccinelle maculée, bien que cette dernière ait présenté un taux de survie minimale de 12,5%. Toutefois, la coccinelle asiatique a survécu entre 25 et

53% dans plusieurs habitations du Québec. Ces résultats suggèrent que la coccinelle asiatique bénéficie d'un espace libre de *froid* (*cold-free space*) lorsqu'elle hiberne dans les maisons, qui serait l'élément-clé du succès d'invasion de cette espèce.

La quantité de ressources (le puceron du maïs *Rhopalosiphum maidis* Fitch) n'a pas influencé la coccinelle asiatique et la coccinelle maculée dans des cages en champ durant deux mois. Toutefois, un impact de la quantité de ressources s'est fait sentir au niveau des premiers stades larvaires de la coccinelle asiatique, plus vulnérables au manque de nourriture, à la prédation et au cannibalisme. Contrairement aux hypothèses de la littérature, les deux espèces, lorsque mises ensembles dans les cages, ont coexisté à tous les niveaux de ressources. De plus, la compétition intraspécifique semblait plus intense que la compétition interspécifique pour les deux espèces. La stratégie d'oviposition des femelles de la coccinelle asiatique, l'incidence assez forte de cannibalisme chez cette espèce et la distribution spatiale différente chez les stades plus vulnérables des deux espèces pourraient expliquer le peu d'effet des ressources sur la coccinelle asiatique et la coexistence avec l'espèce indigène.

Ce doctorat a mis en évidence certaines caractéristiques biologiques de la coccinelle asiatique, des interactions au sein de la communauté aphidiphage et l'influence de certaines variables de l'environnement qui permettent de mieux comprendre les mécanismes d'invasion de cette coccinelle au Québec. L'étude des stades juvéniles des espèces envahissantes devraient être considérées lors des études des mécanismes d'invasion des espèces exotiques. Ce doctorat a permis de mettre en évidence qu'il faut étudier les invasions biologiques sous trois aspects : les caractéristiques biologiques des espèces, des communautés envahies et de l'environnement et les interactions entre eux, afin d'être en mesure de prévenir, prédire et lutte contre ces invasions.

Mots-clés : invasion biologique, *Harmonia axyridis*, *Coleomegilla maculata lengi*, prédation intragilde, développement, survie hivernale, productivité.

INTRODUCTION GÉNÉRALE

1- PROBLÉMATIQUE

Les invasions biologiques représentent une cause majeure du changement global de la planète, amenant des coûts économiques et environnementaux de l'ordre de milliard de dollars chaque année (Colautti *et al.* 2006; Lodge *et al.* 2006; Mack *et al.*, 2000; Pimentel *et al.* 2000; 2001; 2005; Simberloff *et al.*, 2005; Vitousek *et al.*, 1996). Une invasion biologique est l'expansion géographique d'une espèce dans une région qu'elle n'occupait pas auparavant (Vermeij 1996; Williamson 1996). L'augmentation du commerce international, du transfert de denrées d'un pays à l'autre, ainsi que les introductions d'espèces pour la lutte biologique ont amené l'introduction et l'établissement de différentes espèces de plantes et d'animaux qui n'étaient pas présents auparavant, ce qui a grandement altéré la composition et le fonctionnement des écosystèmes terrestres et aquatiques (Dukes et Mooney, 1999; Grosholz 2002). Les invasions biologiques peuvent survenir à la suite d'introductions non intentionnelles, principalement par le transport maritime, aérien ou par voie terrestre (Simberloff 1989; 2005), ou par des introductions délibérées d'ennemis naturels pour le contrôle biologique de ravageurs (Ehler 1998; Simberloff et Stiling 1996). Ces introductions intentionnelles d'ennemis naturels tels que des prédateurs, des parasitoïdes ou des entomophages microbiens, permettent de faire le contrôle biologique de différentes espèces de ravageurs comme des insectes, des mauvaises herbes ou des bactéries (Kimberling 2004). Depuis 1890, il y a eu plus de 2000 introductions délibérées d'arthropodes prédateurs et parasitoïdes pour contrôler des espèces d'insectes ravageurs et d'araignées à travers le monde (Hall *et al.* 1980; Kimberling 2004). De ce nombre, de 2 à 40% de ces espèces auraient eu des impacts sur la communauté indigène (Lodge 1993). Ces introductions délibérées et les nombreuses introductions accidentelles ont amené différents impacts.

Les dommages économiques des espèces envahissantes se retrouvent dans l'industrie agricole, forestière, des pêches, ainsi que par l'introduction de maladies

humaines et du bétail (ACIA 2004; Simberloff *et al.* 2005). La plupart de ces espèces causent des dommages biologiques bien précis : les nouvelles espèces se nourrissent d'espèces natives, changent leurs habitats, compétitionnent avec elles, s'hybrident et les infectent, amenant des déplacements et des extinctions d'espèces ainsi qu'une perte de biodiversité (Pimentel *et al.* 2000; 2005; Simberloff *et al.* 2005). Au Canada, 24% des espèces en péril pourraient être menacées d'extinction par des espèces exotiques envahissantes (ACIA 2004). Les envahisseurs altèrent les fonctions des écosystèmes, comme l'hydrologie et la succession naturelle ou modifient les habitats (Mack *et al.*, 2000; Mooney et Cleland, 2001; Simberloff, 2005).

Quels sont les mécanismes qui permettent à des espèces de s'introduire, de s'établir, de se disperser et de s'intégrer efficacement dans un nouvel environnement? Le succès d'invasion d'une espèce est lié aux caractéristiques de l'espèce, de la communauté et de l'environnement dans lequel elle s'introduit (Keane et Crawley 2002; Kolar et Lodge 2001; Shea et Chesson 2002; Shea *et al.* 2005). Ainsi, des caractéristiques biologiques telles qu'un développement rapide, une grande fécondité et fertilité, de meilleures capacités de recherche de l'hôte ou de la proie, une bonne capacité de dispersion et une meilleure habileté à capturer ses proies vont permettre à la nouvelle espèce de s'installer avec succès dans un nouvel environnement (Kimberling 2004; Reitz et Trumble 2002; Sakai *et al.* 2001). Au sein des communautés, une meilleure capacité à remporter les interactions avec les espèces indigènes et l'absence de prédateurs ou pathogènes du milieu d'origine vont permettre à l'espèce envahissante de s'y installer avec succès (Keane et Crawley 2002; Mack *et al.* 2000; Sakai *et al.* 2001; Shea et Chesson 2002). Ces espèces envahissantes sont souvent meilleures en compétition par exploitation (meilleure capacité de s'approprier les ressources) ou en compétition par interférence, plus particulièrement la prédation intragilde, où l'espèce envahissante se nourrit d'un compétiteur et d'une proie commune (Polis *et al.* 1989; Sakai *et al.* 2001; Yasuda *et al.* 2004). Les caractéristiques de l'environnement vont jouer un grand rôle pour

freiner ou accélérer les invasions biologiques (Mack *et al.* 2000; Von Holle et Simberloff 2005). L'hétérogénéité spatiale, la fragmentation de l'habitat, la productivité du milieu, les perturbations anthropiques ou les caractéristiques abiotiques comme la température, le pH etc. vont influencer le rythme et l'ampleur des invasions (Elton 1958 ; Mack *et al.* 2000 ; Marco *et al.* 2002 ; Stachowicz *et al.* 2002 ; Von Holle et Simberloff 2005 ; With *et al.* 2002). Malgré la somme de connaissances amassées durant la dernière décennie, les invasions biologiques continuent d'augmenter ainsi que les coûts associés à leurs impacts et aux efforts d'éradication. Afin de mieux prédire les risques associés aux invasions biologiques, il faut encore acquérir de l'information sur les traits distinctifs des espèces, des communautés et de l'environnement qui leur permettent de réussir leurs invasions (Simberloff *et al.* 2005).

Au Québec, nous faisons face présentement à l'invasion et l'établissement de la coccinelle asiatique *Harmonia axyridis* Pallas (Coderre *et al.* 1995; Lucas *et al.* 2002; Lucas *et al.* Annexe A). Cette coccinelle a été introduite aux États-Unis comme agent de lutte biologique contre les pucerons et les cochenilles à partir des années 1916, avec des introductions répétées entre les années 1978 et 1982 (Gordon 1985; McClure 1987; Tedders et Schaefer 1994). En 1988, des populations de la coccinelle ont été recensées en Louisiane (Tedders et Schaefer 1994) et en 1994, les premiers individus ont été capturés au Québec dans un verger à Frelishburg (Coderre *et al.* 1995). La coccinelle asiatique présentait des caractéristiques biologiques très intéressantes pour un agent de lutte biologique, soit une grande voracité, un vaste gamme de proies, une très grande fécondité et fertilité (Hodek et Honěk 1996) et une bonne capacité à se disperser (Osawa 1993; 2000). Ces caractéristiques lui permettaient donc de s'introduire et de s'établir aux États-Unis. Toutefois, au début de ce doctorat, les études ne permettaient pas de comprendre précisément quelles caractéristiques de l'espèce lui ont permis d'envahir l'Amérique du Nord avec un si grand succès. Il est aussi apparu que la coccinelle asiatique compétitionnait fortement

avec certaines espèces introduites et indigènes et qu'elle avait le potentiel de déplacer ou de mener à l'extinction certaines espèces natives (Brown et Miller 1998; Colunga-Garcia et Gage 1998; LaMana et Miller 1996), principalement par la prédation intragilde (Hironori et Katsuhiko 1997; Hoogendoorn et Heimpel 2004; Koch 2003; Yasuda *et al.* 2001). Des impacts sur les communautés aphidiphages étaient prévus (Brown et Miller 1998; Reitz et Trumble 2002). Les caractéristiques de l'environnement, particulièrement les températures froides de l'hiver au Québec ou l'hétérogénéité des ressources, pouvaient aussi affecter l'établissement de cette espèce.

L'intérêt de ce travail était autant appliqué que fondamental. Les différents impacts de la coccinelle asiatique sur la communauté pouvaient être évalués et nous pouvions acquérir une meilleure compréhension des invasions biologiques en étudiant plus en profondeur une espèce nouvellement arrivée au Québec. Nous nous sommes donc intéressés à comprendre les différents mécanismes d'invasion de la coccinelle asiatique au Québec, en essayant d'avoir un portrait global des caractéristiques de l'espèce, de la communauté et de l'environnement qui lui permettent son succès d'invasion.

2- ÉTAT DES CONNAISSANCES

2.1 Les invasions biologiques

Les espèces exotiques envahissantes sont des végétaux, animaux ou microorganismes qui ne sont pas indigènes à l'écosystème, qui se sont introduits accidentellement ou ont été introduits volontairement et qui se dispersent dans une région où ils n'étaient pas auparavant (Vermeij 1996; Williamson 1996). Le processus d'invasion est caractérisé par quatre étapes : l'arrivée, l'établissement, l'expansion et l'intégration de l'espèce (Ehler 1998; Vermeij 1996). En premier lieu, l'arrivée de l'espèce peut être non dirigée par les humains, soit par le transport par les courants océaniques, les vents, le transport sur des animaux ou par locomotion active (marche, nage, vol) (Vermeij 1996). Les invasions dirigées par les humains peuvent être par transport accidentel ou intentionnel. L'augmentation du commerce international a accru le transport de marchandises par voie terrestre, maritime et aérienne de semences, plantes, animaux, bois et autres biens de consommation qui peuvent transporter des microorganismes, plantes et animaux exotiques potentiellement envahissants (ACIA 2004; Mack *et al.* 2000; Vermeij 1996). Les voyageurs humains transportent souvent des organismes exotiques entre différents pays, de façon intentionnelle ou non. L'eau de ballast des bateaux relâchée près des côtes est une des voies d'entrées importantes de nombreuses espèces exotiques envahissantes, telles la moule zébrée *Dreissena polymorpha* (Pallas, 1771) dans les Grands Lacs canadiens (Colautti *et al.* 2006). Ainsi, plus de 4500 arthropodes ont été introduits aux États-Unis, dont 95% de façon accidentelle, par les plantes, la terre et l'eau de ballast (Pimentel *et al.* 2005). Les introductions d'agent de lutte biologique sont une voie délibérée d'arrivée d'espèces exotiques envahissantes. En Amérique du Nord, sur 533 espèces d'insectes introduites, 175 se sont établies et 15 ont attaqué des espèces non visées (Simberloff et Stiling 1996). L'horticulture ou l'introduction de

poissons pour la pêche sportive ont accéléré l'introduction délibérée d'espèces exotiques envahissantes (ACIA 2004; Grosholz 2002).

Après l'arrivée de l'espèce exotique, il y a souvent un délai ou une phase de latence, suivie d'une augmentation rapide de la population jusqu'à l'établissement de l'espèce, ce qui complique l'identification des espèces nouvellement arrivées (Ehler 1998; Mack *et al.* 2000). Cette phase de latence peut simplement être due à la croissance normale de la population et à sa distribution, ou peut être due aux changements environnementaux (biotiques et abiotiques) et aux changements génétiques de la population fondatrice qui lui permettra une expansion (Mooney et Cleeland 2001). Il y a établissement quand la nouvelle population peut se soutenir par la reproduction locale et le recrutement (Vermeij 1996). L'établissement d'une espèce peut être affecté par les propriétés de l'espèce et le nombre d'individus introduits, les propriétés des espèces natives et la structure de la communauté ainsi que les conditions biotiques et abiotiques et le niveau de perturbation de l'habitat (Von Holle et Simberloff 2005). D'autres facteurs, comme la quantité de ressource, peuvent influencer l'établissement d'une espèce. Une faible quantité de ressource peut ralentir la croissance de population de l'espèce. Les environnements à faible productivité sont souvent inappropriés pour plusieurs espèces envahissantes car leur succès provient souvent d'une fécondité élevée et d'une croissance de type *r* (Vermeij 1996).

En troisième lieu, l'expansion d'une espèce sera fonction de sa capacité à se disperser, soit de façon naturelle, soit par le transport par les humains. L'expansion peut être facilitée par les perturbations, comme les coupes à blanc, les feux de forêt ou l'urbanisation (Marco *et al.* 2002). La dernière étape d'une invasion biologique est l'intégration. C'est le processus par lequel les espèces dans la communauté réceptrice et l'espèce envahissante répondent les unes aux autres de façon écologique et évolutive. L'espèce envahissante peut modifier l'abondance des espèces indigènes, ce qui modifiera la sélection sur ces espèces. Les envahisseurs établissent rapidement des interactions avec de nouveaux hôtes ou parasites, lesquels vont imposer de

nouveaux contrôles de population et des régimes sélectifs sur les envahisseurs (Hierro *et al.* 2005; Vermeij 1996). L'expansion et l'intégration d'une espèce peuvent être réduites par des contraintes abiotiques comme le climat ou biotiques, comme la présence de compétiteurs, prédateurs ou maladies, l'absence d'hôte, de nourriture ou d'espèces symbiotiques (Vermeij 1996). Peu d'espèces réussissent toutes les étapes d'une invasion et plusieurs ne deviennent jamais envahissantes et problématiques. La règle des 10 de Williamson (1996), bien que contestée, suppose que 1 espèce sur 10 importées apparaît dans le milieu naturel, 1 sur 10 espèces apparues dans le milieu naturel s'établissent et 1 seule espèce sur 10 établies devient problématique.

Les espèces exotiques envahissantes ont des répercussions graves et souvent irréversibles sur les écosystèmes indigènes et sont considérés comme la deuxième menace en importance à la biodiversité après la perte de l'habitat (ACIA 2004; Simberloff 2005). Il y a maintenant autant de plantes envahissantes en Nouvelle-Zélande que d'espèces natives (Mooney et Cleland 2001). Chaque année en Amérique du Nord, on investit des milliards de dollars en mesure d'atténuation des incidences d'espèces exotiques envahissantes (Dawson 2002; Pimentel *et al.* 2005). Ces dépenses comprennent les coûts de prévention des introductions, du contrôle ou de l'éradication des populations de ravageurs, et du rétablissement des habitats après l'application de mesures de contrôle (ACIA 2004). Les coûts attribuables à des espèces envahissantes comprennent la perte de possibilités de commercialisation, la réduction du rendement des cultures exploitables et des coûts accrus de production à cause de l'incidence de ravageurs, ainsi que des baisses de valeur foncière, les coûts de la lutte contre l'incendie, et autres coûts. Les envahisseurs altèrent les fonctions des écosystèmes, comme l'hydrologie et la succession naturelle, délogent et réduisent les populations d'espèces indigènes, modifient les habitats et créent des hybrides avec des espèces indigènes (Mack *et al.*, 2000; Mooney et Cleland, 2001; Simberloff, 2005). Par exemple, le niaouli, *Melaleuca quinquenervia* (Cav.) Blake, une plante envahissante, a remplacé la végétation native sur 160 000 hectares en Floride,

déplacant des espèces d'oiseaux, de mammifères et de reptiles (Schmitz *et al.* 1997). Le coût actuel des dommages causés par les espèces envahissantes affectant la foresterie et l'agriculture au Canada a été estimé à 7,5 milliards de dollars par année (Dawson 2002). Ainsi, les espèces envahissantes coûteraient 314 milliards \$US/an aux États-Unis, Grande-Bretagne, Australie, Afrique du Sud, Inde et Brésil combinés (Colautti *et al.* 2006). Par exemple, la moule zébrée *D. polymorpha*, en plus de compétitionner avec des espèces natives de mollusques et de poissons, cause de sérieux problèmes à l'industrie hydroélectrique en Ontario, car les conduites d'eau infestées par les moules diminuent la puissance hydroélectrique (Colautti *et al.* 2006). De plus, les moules zébrées relâchent de la géosmine qui accroît la croissance des macrophytes et altère le goût de l'eau. La ville de Windsor en Ontario a dépensé entre 400-450 000\$/an pour traiter l'eau au charbon afin d'en éliminer le goût et l'odeur (Colautti *et al.* 2006). La prévention constitue l'élément le plus rentable et le plus productif d'un programme de contrôle des espèces exotiques envahissantes (Mack *et al.* 2000). La détection précoce des envahisseurs aux différents points d'entrée du pays est aussi importante. Cependant, malgré les inspections des différents cargos à la bordure États-Unis et Mexique, seulement 19 à 50% des espèces sont détectées par les inspecteurs (Work *et al.* 2005).

Les évaluations des risques des espèces envahissantes demandent des connaissances sur les caractéristiques des espèces, des communautés et de l'environnement qui pourraient permettre à ces espèces d'envahir nos régions (Byers et Goldwasser 2001; Kimberling 2004; Kolar et Lodge 2001; Marco *et al.* 2002). L'identification des mécanismes principaux du succès d'invasion permettrait de mettre à jour le «talon d'Achille» des invasions, i.e. un aspect de la biologie des envahisseurs ou des interactions avec les espèces natives qui nous permettrait d'intervenir plus rapidement pour limiter efficacement leurs succès ou impacts (Byers et Goldwasser 2001).

2.2 Les mécanismes permettant les invasions biologiques

Le succès d'invasion d'une espèce est fonction de ses caractéristiques et traits d'histoire de vie, des communautés et des caractéristiques de l'environnement (Kolar et Lodge, 2002; Shea et Chesson, 2002; Shea *et al.* 2005; Von Holle et Simberloff 2005). Nous passerons donc en revue les différentes caractéristiques, hypothèses et données empiriques reliées à ces trois aspects.

2.2.1. Les caractéristiques biologiques et traits d'histoire de vie des espèces envahissantes.

Le défi de trouver les caractéristiques biologiques et les traits d'histoire de vie qui confèrent un succès d'invasion reste encore important, malgré de nombreuses études (Elton 1958; Kolar et Lodge 2001; Mack *et al.* 2000; Sakai *et al.* 2001; Shea *et al.* 2005). Les espèces envahissantes présentent généralement un taux de reproduction élevé, un taux de croissance de population rapide, combinés avec une grande capacité de dispersion (Kimberling 2004; Kolar et Lodge 2001; Reitz et Trumble 2002; Sakai *et al.* 2001; Shea *et al.* 2005). Les espèces envahissantes, qui sont souvent de plus grande taille que les espèces natives, ont aussi plus de chances de s'installer avec succès dans le nouvel environnement car ils peuvent atteindre une plus grande fécondité et une plus grande densité de population (Byers 2000). Quand on s'intéresse plus précisément aux prédateurs, les espèces envahissantes sont généralement polyphages, synchronisées avec leurs proies de prédilection au niveau temporel, ont une grande efficacité de recherche des proies, et peuvent persister sans leur proie de prédilection (Kimberling 2004; Reitz et Trumble 2002; Sakai *et al.* 2001). Les espèces qui présentent une plus grande survie aux stades juvéniles de croissance ainsi qu'au stade adulte ont aussi plus de chances de s'établir (Kolar et Lodge 2001; Marco *et al.* 2002; Shea *et al.*, 2005). Par exemple, le moustique du Tigre d'Asie *Aedes albopictus* (Skuse), récemment introduit en Floride, a montré

qu'il prenait moins de temps à éclore qu'une espèce native *A. triseriatus* (Say), et que les larves se développaient plus rapidement (Lounibos *et al.* 2001).

Ces espèces présentent en général une grande plasticité phénotypique, i.e. la production de plusieurs phénotypes provenant d'un seul génotype, dépendant des conditions environnementales (Miner *et al.* 2005). Les individus plastiques sont capables de s'adapter rapidement à de nouvelles situations, en changeant leurs comportements, leur physiologie, morphologie, croissance et démographie dans leur nouvel environnement (Blossey et Nötzold 1995; Miner *et al.* 2005; Sakai *et al.* 2001; Sol et Lefebvre 2000). Une espèce envahissante peut apprendre, améliorer ses processus cognitifs ou s'ajuster rapidement aux nouvelles conditions du milieu, ce qui lui confère un avantage pour survivre et se reproduire (Sol et Lefebvre 2000; Sol *et al.* 2002). Il a été démontré que le succès d'invasion d'oiseaux en Nouvelle-Zélande était corrélé avec la taille de leur cerveau et leur capacité d'innover pour trouver de la nourriture (Sol et Lefebvre 2000; Sol *et al.* 2002). Les invasions réussies semblaient liées à la capacité de ces espèces à exploiter une grande variété de milieux. Holway et Suarez (1999) ont démontré que la fourmi envahissante *Solenopsis invicta* Buren a changé ses comportements dans le nouvel environnement. Dans leur pays d'origine, deux formes de colonies sont présentes; les colonies monogynes, où il n'y a qu'une seule reine, et les colonies polygynes avec plusieurs reines apparentées génétiquement. Dans les régions envahies, les colonies polygynes acceptent les reines non apparentées, augmentant ainsi les densités de population, avec le potentiel de s'attaquer et déplacer beaucoup plus d'espèces natives (Holway et Suarez 1999). La fourmi d'Argentine, *Linepithema humile* (Mayr, 1868), montre elle aussi des changements de comportement après son introduction. Dans son pays d'origine, les fourmis présentent une grande agressivité intraspécifique entre les colonies à petite échelle spatiale. Par contre, en Californie et au Chili, très peu d'agressivité a été observée, ce qui permet l'établissement de plus grosses colonies (Holway 1998; Holway et Suarez 1999). Cette forte densité d'individus est très importante pour la

capacité de cette fourmi à effectuer de la compétition par exploitation des ressources et par interférence. L'étude du comportement des espèces envahissantes devrait donc prendre une part importante des études sur les invasions biologiques (Holway et Suarez 1999; Holway et Case 2001).

La quantité d'individus introduits serait aussi une caractéristique importante pour déterminer le succès d'invasion et d'établissement (*propagule pressure*; Kolar et Lodge 2001; Lonsdale 1999; Mack *et al.* 2000; Von Holle et Simberloff 2005; Williamson 1996). Plusieurs expériences manipulatives ont démontré que le nombre de graines de plantes qui arrivaient dans le nouvel environnement expliquait leur succès d'invasion (Hierro *et al.*, 2005; Turnbull *et al.*, 2000; Von Holle et Simberloff, 2005). Von Holle et Simberloff (2005) ont récemment démontré en milieu littoral que la pression exercée par la quantité de plantes envahissantes au départ était plus importante pour le succès d'invasion que la diversité des espèces natives ou les caractéristiques physiques de l'habitat.

Certaines espèces peuvent aussi devenir dominantes dans le milieu après leur invasion par des changements génétiques rapides à la suite de nouvelles pressions de sélection dans le nouvel environnement (Hänfling et Kollman 2002; Hierro *et al.* 2005; Lee 2002; Mooney et Cleland 2001; Sakai *et al.* 2001; Stockwell *et al.* 2003). Les facteurs biotiques et abiotiques du nouvel environnement peuvent devenir des forces sélectives importantes (Lee 2002; Stockwell *et al.* 2003). L'algue tropicale envahissante *Caulerpa taxifolia* (Vahl) C. Agardh a développé une tolérance à l'eau froide quand elle était en croissance à l'aquarium du zoo de Stuttgart et autres aquariums privés et publics (Mack *et al.* 2000). Depuis ce temps, elle s'est échappée dans la Méditerranée du Nord-Ouest, et son adaptation à l'hiver lui a permis de remplir de vastes étendues de mer, causant des dommages aux espèces natives (Mack *et al.* 2000). Une évolution rapide peut survenir en présence de nouveaux organismes compétiteurs ou en leur absence. Ainsi, l'hypothèse de l'évolution de l'habileté compétitrice (*evolution of increased competitive ability hypothesis- EICA*), suppose

que les espèces exotiques libérées de leurs ennemis spécialistes vont perdre les traits coûteux qui leur donnaient une certaine résistance aux ennemis (Blossey et Nötzold 1995). Les espèces envahissantes peuvent donc utiliser les ressources qui étaient autrefois allouées à la résistance afin d'augmenter leur taille ou leur fécondité. Par exemple, Leger et Rice (2003) ont démontré que le pavot de Californie, *Eschscholzia californica* Cham. provenant du Chili était plus large et plus fécond que les conspécifiques californiens dans les jardins, mais seulement en absence de compétition. Une étude sur la salicaire pourpre a montré qu'elle devenait plus grande dans le pays envahi que dans son pays d'origine (Blossey et Nötzold 1995). Par contre, les génotypes exotiques du millepertuis *Hypericum perforatum* L., n'étaient pas plus féconds ou plus larges que les espèces natives, malgré une réduction dans leur résistance aux pathogènes et dans leur défense chimique (Maron *et al.* 2004). Cette hypothèse reste encore à tester en comparant les caractéristiques des espèces exotiques dans leur milieu d'origine et dans le milieu envahi (Hierro *et al.* 2005).

Malgré ces études, il est encore difficile de déterminer les caractéristiques biologiques et traits d'histoire de vie communes aux espèces envahissantes qui nous permettraient de mieux prédire les invasions et leurs impacts (Simberloff *et al.* 2005).

2.2.2. Les caractéristiques des communautés envahies et le succès d'invasion

Lorsque les espèces sont établies et commencent à s'étendre, les interactions au sein des communautés vont jouer un grand rôle dans le succès d'invasion des espèces exotiques (Shea et Chesson 2002). La présence de niches vides, la compétition avec les espèces natives et la présence ou l'absence d'ennemis naturels vont influencer l'expansion et l'établissement de ces espèces. De plus, lorsque l'espèce envahissante aura atteint une certaine densité, elle aura des effets sur les communautés locales, en consommant les ressources et en maintenant les ennemis naturels (Shea et Chesson 2002).

Certaines espèces envahissantes peuvent survivre dans le nouveau milieu car elles ont accès à des ressources dans la communauté qu'aucune espèce utilise, aussi appelée hypothèse des niches vides (Elton 1958; Levine et d'Antonio 1999; MacArthur 1970; Mack *et al.* 2000). Par exemple, le canard mandarin *Aix galericulata* L. aurait réussi à envahir la Grande-Bretagne, du fait qu'il a occupé une niche alimentaire vacante car il mangeait principalement des vertébrés aquatiques au printemps et durant l'été, et des glands et châtaignes l'automne et l'hiver (Long 1981). Une hypothèse associée à celle-ci est celle de l'opportunisme écologique, qui explique le succès d'invasion par le fait que des extinctions d'espèces, et donc la création de niches, promeut l'établissement des espèces envahissantes. Cette hypothèse a été vérifiée pour l'introduction de poissons (Christie 1974) et d'oiseaux (Diamond et Veitch 1981). De plus, la susceptibilité d'une communauté à l'invasion augmente lorsque la quantité de ressources inutilisées augmente (Davis *et al.* 2000). Par exemple, la centauree du solstice, *Centaurea solstitialis* L., domine maintenant les prairies de Californie. Sa dominance après son introduction pourrait être due à la présence d'eau interstitielle inutilisée à 60 cm de profondeur du sol. Les racines plus longues de cette mauvaise herbe ainsi que la sénescence plus rapide des plantes indigènes lui confèreraient une meilleure exploitation des sites et de ressources inutilisées (Dyer et Rice 1999; Holmes et Rice 1996).

Elton (1958) fut le premier à proposer la notion que les communautés plus diversifiées en espèces seraient plus résistantes aux invasions que les moins riches. Les communautés de faible richesse spécifique présentent moins d'interactions interspécifiques et plus de niches vides (Crawley 1987; Drake 1990; MacArthur 1970). L'utilisation des ressources serait donc réduite dans les communautés à faible richesse et la présence de ressources inutilisées pourraient rendre les communautés pauvres plus facilement envahies que les communautés riches (Crawley 1987; Tilman *et al.* 1996). Plusieurs expériences manipulatives supportent l'idée que la diversité augmente directement la résistance des communautés à l'invasion (Levine 2000;

Naeem *et al.* 2000; Stachowicz *et al.* 1999; 2002). Stachowicz *et al.* (2002) ont démontré que la réduction de la diversité d'espèces d'invertébrés (anémones, hydroïdes, ascidies, éponges) amenait une augmentation du pourcentage final d'espèces envahissantes. Toutefois, cette hypothèse de diversité-invasion reste encore à vérifier, car les résultats diffèrent; soit les communautés plus diverses sont plus envahies, soit elles le sont moins (Hierro *et al.* 2005), des résultats qui seraient principalement dus à l'échelle d'expérimentation (Tilman 1999).

Les différentes interactions entre les espèces indigènes et les espèces envahissantes influencent l'établissement et l'expansion de ces dernières (Corbin et d'Antonio 2004). Dans une communauté, les individus peuvent avoir un effet négatif dans l'accès aux ressources de façon indirecte, i.e. en compétition par exploitation (s'accapare les ressources avant l'autre espèce), ou de façon directe, en compétition par interférence (attaque, tue, mange l'autre espèce) (Connell 1980; Welden et Slausen 1986), qui peuvent amener une diminution de la fécondité, de la survie ou de la croissance d'un individu d'une espèce (Begon *et al.* 1996). Ces différents types de compétition vont affecter la dynamique de population des espèces compétitrices, ce qui va influencer la distribution des espèces et leur évolution. Si les ressources ne sont pas séparées de façon temporelle ou spatiale, les espèces qui présentent des besoins similaires en ressources ou habitats vont compétitionner intensément, ce qui pourrait mener à l'exclusion d'une espèce (Bando 2006; Begon *et al.* 1996; Dudgeon *et al.* 1999; Reitz et Trumble 2002).

Une compétition par exploitation peut s'établir pour différentes ressources, par exemple pour l'espace, comme les bons sites de germination chez les plantes (Marco *et al.* 2002) ou un substrat pour s'attacher et profiter des courants d'eau amenant les particules en suspension pour les anémones (Stachowicz *et al.* 2002). La capacité de trouver plus rapidement la ressource chez les animaux mobiles pourrait permettre à l'espèce envahissante de s'accaparer la nourriture et réduire la survie de l'espèce native qui se nourrit de la ressource. Byers (2000) a démontré qu'une espèce

d'escargot japonais envahissant, *Batillaria attramentaria* (Sowerby II, 1855), excluait l'escargot natif *Cerithidea californica* (Haldeman, 1840). L'escargot exotique avait un avantage en compétition par exploitation par sa plus grande efficacité de conversion des diatomées en biomasse et capacité reproductrice. Le moustique exotique *A. albopictus*, récemment installé en Floride, est une espèce supérieure au moustique natif *A. triseriatus* du fait de son utilisation plus efficace des ressources au stade larvaire, ce qui amène un déplacement de l'espèce native (Lounibos *et al.* 2001). Les études sur les invasions biologiques permettent de mieux comprendre les mécanismes de compétition interspécifique, qu'il est difficile d'évaluer dans un milieu où la compétition s'est stabilisée dans le temps (Holway 1999; Lodge 1993; Petren et Case 1996; Sakai *et al.* 2001).

La compétition par interférence est aussi très fréquente entre les envahisseurs et les espèces natives. Par exemple, la fourmi de feu *S. invicta* a réduit la diversité des fourmis natives de 70% et la diversité d'autres arthropodes de 30% en attaquant et tuant les arthropodes qu'elle rencontrait (Porter et Savignano, 1990). Les interactions trophiques complexes, comme la prédation intragilde et le cannibalisme, sont très communes dans les chaînes trophiques (Holt et Polis 1997; Lucas 2005; Polis 1991; Polis *et al.* 1989; Polis et Holt 1992; Woodward et Hildrew 2001). L'exemple le plus simple de prédation intragilde est une configuration de 3 espèces : un prédateur, un consommateur intermédiaire et une ressource. Le prédateur mange la ressource et le consommateur intermédiaire, tandis que le consommateur intermédiaire se nourrit de la ressource (Figure 1). On peut retrouver aussi une prédation intragilde mutuelle, où il y a une prédation mutuelle entre le consommateur intermédiaire et le prédateur. La prédation intragilde se distingue des concepts traditionnels de la compétition par le gain énergétique immédiat d'un des participants et diffère de la prédation classique par le fait qu'elle réduit la compétition (Polis *et al.* 1989; Polis et Holt 1992). Différents paramètres influencent la prédation intragilde (voir Lucas 2005): la taille des individus, le mouvement des individus (sessile, peu mobile, mobile) (Lucas *et al.*

1998), la présence et l'absence de proies extragilde (Agarwala et Dixon 1992; Lucas *et al.* 1998; Osawa 1992; Polis *et al.* 1989), la quantité de proies disponibles (Dielh et Feissel 2000; Hironori et Katsuhiko 1997; Lucas *et al.* 1998), le comportement d'agressivité et de dispersion (Hironori et Katsuhiko 1997; Schellhorn et Andow 1999), la niche d'oviposition (Coderre *et al.* 1987; Dixon 2000; Hemptinne *et al.* 1992), la complexité du milieu (Finke et Denno 2002; Menge et Sutherland 1976; Petren et Case 1998) et la productivité du milieu (quantité de ressource) (Abrams 2001; Diehl et Feissel 2000; Holt et Polis 1997; Morin 1999; Mylius *et al.* 2001; Polis *et al.* 1989; Revilla 2002). La prédation intragilde a été observée chez les mammifères (Laursen 1994), les oiseaux (Wright 1981), les reptiles (Wright 1981), les poissons (Dion et Whoriskey 1993), les amphibiens (Burley *et al.* 2006; Gustafson 1993) et les invertébrés (Polis *et al.* 1989). Les espèces envahissantes prédatrices effectuent souvent de la compétition par interférence et de la prédation intragilde (Brown et Miller 1998; Holway 1998; 1999; Hoogendoorn et Heimpel 2004). Le gecko *Hemidactylus frenatus* Fitzinger a réduit l'espèce native *Lepidodactylus lugubris* (Duméril et Bibron 1836) après son invasion dans les îles du Pacifique par son exploitation plus grande des ressources en insecte et de façon indirecte en compétition par interférence (Petren et Case 1996). La diète alimentaire des deux espèces était pratiquement la même et l'espèce native réduisait son activité de recherche de nourriture en présence de l'espèce envahissante, ce qui se traduisait par une diminution de l'acquisition de nourriture et une diminution de la croissance de population. La fourmi d'Argentine *L. humile*, compétitionne avec les fourmis natives autant par la compétition par exploitation, en s'appropriant plus rapidement les ressources, que par compétition par interférence, en attaquant les fourmis natives (Holway 1999).

Les espèces natives peuvent aussi résister aux invasions par leur habiletés compétitrices (Grosholz 2002). Ce fut le cas dans les estuaires de San Diego, où la moule asiatique *Musculista senhousia* (Benson in Cantor, 1842) subissait une plus

grande prédation par les invertébrés benthiques natifs que dans son milieu d'origine (Reusch 1998; Reusch et Williams 1999). La plante hydrophyte *Zostera marina* L. était aussi efficace en limitant la croissance et l'expansion de la moule envahissante (Reusch et Williams 1999).

Il existe aussi un autre type de compétition indirecte, appelée la compétition apparente, où plusieurs prédateurs vont être attaqués par un même ennemi (Holt et Lawton 1994), par exemple un parasitoïde. Lorsqu'un des compétiteurs est plus attaqué par l'ennemi commun, la pression de prédation plus forte le rend moins compétitif, ce qui donne un avantage à l'autre espèce. La compétition apparente peut aussi influencer le succès d'invasion (Hoogendoorn et Heimpel 2002; Settle et Wilson 1990). Settle et Wilson (1990) ont observé un déclin des populations de la cicadelle de la vigne-vierge *Erythroneura elegantula* (Osborn) à la suite de l'invasion de la cicadelle *Erythroneura variabilis* Beamer en Californie. Ce déclin serait dû à des taux différents de parasitisme de l'espèce indigène et envahissante. La présence de l'espèce envahissante aurait permis aux populations de parasitoïdes de croître. Cependant, les parasitoïdes attaquent plus efficacement l'espèce native que l'espèce envahissante, ce qui a conduit au déclin de l'espèce native. Dans certains cas cependant, l'introduction d'un nouvel hôte peut diminuer le parasitisme sur l'hôte indigène (Müller et Godfray 1999).

Un des mécanismes d'invasion des espèces envahissantes au sein des communautés est le relâchement de la pression par les ennemis naturels (*enemy release hypothesis*) (Keane et Crawley 2002). Ainsi, une espèce nouvellement introduite dans l'environnement aura une pression de prédation moins forte, son abondance devrait augmenter et sa distribution s'étendre rapidement. Cette théorie s'appuie sur trois arguments : 1) les ennemis naturels sont d'importants régulateurs des populations ; 2) les ennemis naturels ont un plus grand impact sur les espèces natives que sur les espèces envahissantes et 3) les espèces envahissantes peuvent exploiter cette réduction de la pression des ennemis naturels et augmenter ainsi leur

croissance de population (Keane et Crawley 2002). Carpenter et Cappucino (2005) ont mesuré l'intensité de l'herbivorie sur 39 espèces de plantes envahissantes et 30 espèces natives dans des habitats naturels près d'Ottawa au Canada. L'herbivorie était moins intense sur les espèces envahissantes, confirmant ainsi l'hypothèse du relâchement des ennemis naturels sur les espèces envahissantes. Colautti *et al.* (2005) ont observé une certaine réduction des parasites attaquant les étourneaux sansonnets d'Europe (*Sturnus vulgaris* L.) après leur introduction en Amérique du Nord. Cependant, les données présentes montrent que plusieurs parasites natifs s'attaquent maintenant à cette espèce, équilibrant ainsi le nombre de parasites entre le milieu natif et d'introduction (Colautti *et al.* 2005). Cette hypothèse reste toutefois encore à vérifier.

2.2.3 L'influence des caractéristiques de l'environnement sur le succès d'invasion

Les organismes habitent dans des environnements présentant plusieurs dimensions qui peuvent varier de façon spatiale et temporelle (Ancel Meyers et Bull 2002) et influencer le succès d'invasion des espèces envahissantes. Ainsi, les caractéristiques abiotiques, (pH, température, type de sol, concentration d'oxygène dans l'eau etc.), les caractéristiques biotiques (productivité du milieu), la structure de l'habitat (hétérogénéité spatiale, fragmentation de l'habitat...) ou les perturbations anthropiques vont influencer le rythme et l'ampleur des invasions (Elton 1958 ; Mack *et al.* 2000 ; Marco *et al.* 2002 ; Stachowicz *et al.* 2002 ; Von Holle et Simberloff 2005 ; With *et al.* 2002). Le succès d'invasion d'une espèce en regard des caractéristiques de l'environnement sont cependant généralement liées aux caractéristiques biologiques de l'espèce et aux interactions avec la communauté. Les études récentes démontrent qu'il faut évaluer le succès d'invasion des espèces envahissantes, non seulement au sein des communautés, mais combinées à des gradients environnementaux (Von Holle 2005).

Les caractéristiques abiotiques, telles le pH, la température, le type de sol, la concentration d'oxygène de l'eau, etc. peuvent empêcher ou favoriser l'invasion d'une espèce. Ces caractéristiques de l'environnement sont bien sûr liées aux caractéristiques des espèces (Kolar et Lodge 2001). Les espèces envahissantes ne peuvent s'établir dans un environnement où les conditions abiotiques ne sont pas adéquates (Lodge 1993). Elles peuvent cependant s'adapter à ces conditions et réussir à s'établir après un certain temps (Simberloff *et al.* 2005). L'algue tropicale envahissante *C. taxifolia*, qui s'est adaptée tranquillement aux températures plus froides de l'eau et qui envahit maintenant la Méditerranée en est un exemple (Mack *et al.* 2000). Les caractéristiques semblables entre le milieu envahi et le milieu d'origine peuvent donc permettre à l'espèce de s'établir et de devenir envahissante (Kolar et Lodge 2001).

Nous avons discuté plus tôt de l'influence des ressources sur la disponibilité des niches pour les espèces envahissantes et de la compétition qui peut survenir avec les espèces natives. Cependant, nous pouvons aussi définir une des caractéristiques biotiques de l'environnement comme la productivité du milieu, c'est-à-dire la quantité de ressources. Ces ressources peuvent être la quantité de productivité primaire, de nutriments, la quantité de proies, l'espace etc. La productivité du milieu peut influencer le succès d'établissement d'une espèce dans le milieu (Kiesecker *et al.* 2001; Tilman 1997; 1999). Stachowicz *et al.* (2002) ont montré que le succès d'invasion d'invertébrés benthiques était relié, en plus de la diversité des espèces natives, à la disponibilité des ressources. Dans leurs expériences, les ressources étaient la quantité d'espace disponible pour que les invertébrés puissent se fixer au substrat et avoir accès à la nourriture en suspension. Lorsque la disponibilité des ressources était faible, il y avait une plus faible proportion d'espèces envahissantes qui réussissaient à s'établir. La salicaire pourpre, *Lythrum salicaria* L., présente une plus grande fécondité dans les milieux plus riches en nutriments dans les milieux envahis que dans des habitats riches dans son milieu d'origine (Edwards *et al.* 1998).

La compétition par interférence, particulièrement la prédation intragilde, peut être influencée par la quantité de ressource du milieu (Abrams 2001; Diehl et Feissel 2000; Holt et Polis 1997; Morin 1999; Mylius *et al.* 2001; Polis *et al.* 1989; Revilla 2002). Plusieurs études théoriques supportées par des données empiriques ont montré 1) qu'une espèce meilleure en compétition par exploitation devrait avoir une meilleure survie quand les ressources sont en faible quantité, 2) que les espèces avec une plus grande habileté de compétition par interférence et de prédation intragilde vont survivre mieux à forte quantité de ressource, et 3) que la coexistence entre les espèces sera possible à un niveau de ressource intermédiaire (Diehl et Feissel 2000; 2001; Morin 1999; Mylius *et al.* 2001). Ainsi, la proie intragilde, meilleure en compétition par exploitation, réussit à survivre en présence d'une faible quantité de ressource dans le milieu car elle s'accapare les ressources (Holt et Polis 1997). À forte quantité de ressources, le prédateur intragilde va mener l'autre espèce à l'extinction car il effectue une plus grande pression de prédation et de compétition. Par contre, peu d'études ont évalué l'impact de la prédation intragilde sous différents niveaux de productivité du milieu et l'impact des ressources et de la prédation intragilde sur le succès des espèces envahissantes (Chase 1996; Müller et Brodeur 2002).

Le succès d'invasion peut aussi dépendre de l'interaction entre la distribution des ressources, les habiletés compétitives et le régime de perturbation (MacDougall et Turkington 2005; Kiesecker *et al.* 2001). Le ouaouaron envahissant *Rana catesbeiana* Shaw a contribué à la réduction des populations de la grenouille à pattes rouges *Rana aurora* Baird et Girard en Orégon aux États-Unis (Kiesecker *et al.* 2001). La compétition entre les deux espèces était liée à la distribution des ressources : lorsque la nourriture était groupée, la présence du ouaouaron diminuait la recherche active des grenouilles, qui ne pouvaient s'alimenter et mouraient. Par contre, lorsque les ressources étaient dispersées, les grenouilles avaient un meilleur taux de survie. La modification des milieux humides partout en Amérique du Nord pourrait jouer un

rôle dans la diminution de la grenouille à pattes rouges, car la réduction de la grandeur des mares augmente l'aggrégation des ressources, augmentant par le fait même les interactions possibles entre l'espèce envahissante et l'espèce native (Kiesecker *et al.* 2001).

L'hétérogénéité spatiale peut procurer des refuges aux espèces natives et permettre à celles-ci de résister aux invasions. Par exemple, l'ajout de structures verticales sur les murs des bâtiments où le gecko envahissant *H. frenatus* était mis en présence du gecko natif *L. lugubris* a diminué la compétition entre les deux espèces (Petren et Case 1996). Le gecko envahissant ne pouvait plus détecter l'espèce native lorsqu'elle chassait les insectes, ce qui a diminué les interactions entre les deux espèces, et permis à l'espèce native de survivre. L'occupation de l'espace par les espèces natives serait la clé pour augmenter la résistance aux invasions (Stachowicz *et al.* 2002). Ainsi, lorsque le milieu est stable, autant au niveau spatial que temporel, la résistance à l'invasion semble plus grande (Stachowicz *et al.* 2002). Cependant, les perturbations occasionnées par les humains pourraient jouer un grand rôle dans la capacité d'invasion des espèces exotiques et dans l'augmentation des invasions biologiques.

La perte d'habitat, la déforestation, la pollution de l'eau sont des perturbations de l'habitat qui peuvent agir de façon additive ou synergique avec les invasions biologiques et causer des impacts plus grands sur la biodiversité des espèces natives (Didham *et al.* 2005 ; Hood et Naiman 2000). Le brome des toits, *Bromus tectorum* L., s'est montré plus envahissant dans les environnements fragmentés de l'ouest des États-Unis, altérant les régimes de feu, ce qui a augmenté la fragmentation, et ainsi l'invasion subséquente de la plante (Knick et Rotenberry 1997). Dans une autre étude, la compétition entre des fourmis natives et envahissantes en Californie a été influencée par la proximité des régions urbaines, et donc par le degré de fragmentation (Suarez *et al.* 1998). Il n'est pas clair toutefois si les invasions se produiraient à une aussi grande échelle et avec d'aussi grands impacts si l'habitat

n'avait pas été modifié auparavant. Gurevitch et Padilla (2004) ont noté que les déclin et les extinctions d'espèces de moules étaient déjà fréquentes avant l'invasion de la moule zébrée dans les Grands Lacs. Les perturbations peuvent encourager les invasions si les espèces natives ne peuvent s'acclimater ou s'adapter à celles-ci (Byers 2002; Mack *et al.* 2000). Byers (2002) suggère que les perturbations anthropogéniques, qui peuvent survenir sur quelques années ou quelques jours, pourraient être trop rapides pour que les espèces natives puissent y répondre de façon évolutive. Elles perdraient donc leurs avantages sur les espèces envahissantes. Des perturbations de l'habitat comme les feux de forêt, les inondations, les pratiques agricoles, le pâturage d'animaux d'élevage, le drainage des milieux humides ou l'altération de la salinité sont d'autres facteurs permettant les invasions biologiques (Mack *et al.* 2000). Bando (2006) a effectué une expérience où il a perturbé l'habitat en détruisant les plantes déjà présentes sur les bordures de rivière, qui mimait la perturbation d'un bateau à moteur arrachant les plantes flottantes par exemple. Il a pu démontrer que l'espèce envahissante de plante hydrophyte *Zostera japonica* Aschers. and Graebn. était plus performante que l'espèce native *Z. marina* L. lorsque l'habitat était perturbé.

Les caractéristiques de l'habitat peuvent donc influencer grandement les espèces envahissantes, par les conditions abiotiques ou biotiques qu'elles rencontrent, ce qui peut expliquer en partie leur succès d'invasion. Ces caractéristiques sont cependant généralement indissociables des caractéristiques biologiques des espèces et des interactions au sein des communautés, ce qui demande d'effectuer des études qui mesurent cette interaction espèce x communauté x environnement afin de mieux comprendre les mécanismes d'invasion des espèces envahissantes.

2.3-Les coccinelles et les invasions biologiques

Les coccinelles prédatrices sont utilisées très souvent dans le contrôle biologique du fait qu'elles sont des prédateurs importants de plusieurs espèces de ravageurs, spécialement les mouches blanches, les pucerons, les cochenilles et les acariens (DeBach et Rosen 1991; Obrycki et Kring 1998) et ont de meilleures capacités que d'autres groupes d'ennemis naturels à s'installer dans les habitats perturbés et sur les cultures maraîchères (Hodek et Honěk 1996). À partir de 1889, de nombreuses espèces de coccinelles ont été introduites comme agent de lutte biologique. *Rodolia cardinalis* (Mulsant) fut la première coccinelle introduite en 1889 pour contrôler la cochenille *Icerya purchasi* (Maskell) qui infestait les vergers d'agrumes en Californie (Turnbull et Chant 1961). Ce fut une réussite phénoménale et la cochenille fut rapidement contrôlée. Sous l'égide de cette réussite, de nombreuses introductions de parasitoïdes et de prédateurs ont été effectuées dans l'espoir de contrôler des espèces de ravageurs exotiques sur des cultures comme les olives, les citrons, la luzerne et le maïs (Caltagirone et Doult 1989; Obrycki et Kring 1998; Pimentel *et al.* 1984). Durant les 100 dernières années, plus de 40 espèces de coccinelles ont été introduites en Amérique du Nord (Caltagirone 1981), avec un taux de succès d'établissement assez faible (9%) (Gordon 1985; Lodge 1993; Waage 1990; Williamson 1996). Ainsi, les coccinelles à onze points, *Coccinella undecimpunctata* L., à sept points *Coccinella septempunctata* L., la coccinelle asiatique *H. axyridis*, *H. dimidiata* (F.), *H. quadripunctata* (Pontoppidan, 1763), la coccinelle variée *Hippodamia variegata* (Goeze), et la coccinelle à 14 points *Propylea quatuordecimpunctata* L. ont été introduites et se sont établies avec succès. Cependant, il n'est pas clair si elles se sont établies à la suite des programmes d'introduction ou par introduction accidentelle dans les ports (Krafsur *et al.* 2005).

Malgré le succès de *R. cardinalis*, les introductions d'autres espèces de coccinelles n'ont pas toutes été fructueuses et certaines se sont soldées par des impacts négatifs sur d'autres espèces. Par exemple, G.W. Angalet a introduit la

coccinelle à sept points *C. septempunctata* en Californie en 1959 (Butler 1982) et plusieurs autres introductions ont eu lieu par la suite dans divers états des États-Unis (Angalet *et al.* 1979). Elle se retrouve maintenant communément au Québec et au Canada (Coderre 1983; Lucas *et al.* Annexe A; Turnock *et al.* 2003). Les effets négatifs de la coccinelle à sept points sur les coccinelles indigènes ont été documentés durant 18 années au Dakota du Sud par Elliott et Kieckhefer (1990), Kieckhefer *et al.* (1992) et Elliott *et al.* (1996). À la suite de l'invasion de la coccinelle asiatique, ils ont observé une diminution sévère de la densité de certaines espèces de coccinelles telles que *Coccinella transversoguttata ridcharsoni* Brown et *Adalia bipunctata* L., qui semblait liée aux interactions compétitives et à la prédation intraguilde sur les espèces natives (Elliott *et al.* 1996). L'invasion de la coccinelle à sept points en Amérique du Nord semble aussi impliquée dans la réduction générale de la coccinelle à neuf points *Coccinella novemnotata* Herbst et *Hippodamia convergens* Guérin-Ménéville (Wheeler et Hoebeke 1995; Ellis *et al.* 1999). La coccinelle à 14 points *P. quatuordecimpunctata*, une autre espèce envahissante fut observée pour la première fois près de Québec en 1968 et s'est ensuite répandue dans le Nord-Est des États-Unis (Day *et al.* 1994; Gordon 1985). Sa présence dans les champs de pommes de terre dans le Maine aux États-Unis a été associé à une diminution de la présence de la coccinelle à bandes transverses, *C. transversoguttata* (Alyokhin et Sewell 2004). Toutefois, très peu d'études ont été effectuées sur cette espèce et sur les impacts qu'elle a pu générer à la suite de son introduction. La coccinelle variée, *H. variegata*, s'est établie près de Montréal, au Québec, avant 1984 (Gordon 1987). En 1992, cette espèce était distribuée du nord du New Jersey jusqu'à New York. Elle s'est étendue au sud du Nouveau-Brunswick et à l'île du Prince-Édouard en 1993 et 1995 respectivement (Hoebeke et Wheeler 1996). Peu d'études ont été effectuées sur cette espèce et les caractéristiques de son succès d'invasion ne sont pas connues.

Le taux d'établissement des coccinelles en Amérique du Nord (0,10) est beaucoup plus faible que le taux estimé pour les programmes de lutte biologique dans

le monde (0,34) (Waage 1990). Le succès d'invasion des coccinelles a été peu étudié (Obrycki et Kring 1998). Une étude de Phoofole et Obrycki (1995) sur la coccinelle à sept points a permis de montrer qu'une grande plasticité dans la fécondité et la période d'oviposition des femelles a pu contribuer à son grand succès d'invasion. Sa grande taille, sa voracité et son habileté à compétitionner par interférence, principalement par la prédation intragilde, lui aurait permis de compétitionner avec les espèces natives et de s'installer avec succès dans le nouvel environnement (Cottrell et Yeargan 1999; Evans 1991). De plus, Evans (2004) a suggéré que la coccinelle à 7 points diminuait grandement les quantités de pucerons dans les champs, ce qui diminuait l'attrance des coccinelles natives adultes. Ces dernières ne feraient donc que passer dans les champs, ne s'y reproduisant pas. La coccinelle à sept points arrive aussi plus tôt dans les champs, ce qui peut augmenter la prédation intragilde sur les espèces natives (Evans 2004). Les interactions entre les larves de coccinelles natives et de la coccinelle à sept points pourraient être un mécanisme contribuant au succès de cette espèce.

2.4- La coccinelle asiatique, *Harmonia axyridis* Pallas

La coccinelle asiatique *H. axyridis* est largement distribuée en Asie. On la retrouve à Formose, en Chine, en Corée, au Japon, en Sibérie du Sud et aux Iles Bonin et Ryuku (Chapin et Brou 1991). Cette espèce semi-arboricole se retrouve dans les vergers, les forêts de conifères (McClure 1986) et les forêts décidues (Chapin et Brou 1991), mais aussi dans les jardins et les champs d'annuelles (Hodek 1973; Schanderl *et al.* 1985; Schanderl 1987) et est polyphage (Hodek 1973; Koch 2003; Pervez et Omkar 2006; Tedders et Schaefer 1994). Cette espèce est polymorphique (Soares 2000), très prolifique, est multivoltine dans sa contrée d'origine (Osawa 2000) et peut vivre plus de trois ans (Hodek 1973). Cette espèce avait été choisie comme agent de lutte biologique des pucerons à cause de sa taille, de son vaste régime alimentaire, de son efficacité de prédation et de son habileté de colonisation de divers habitats (Majerus *et al.* 2006). Il y a eu plusieurs tentatives d'introduction de la coccinelle asiatique en Amérique du Nord depuis 1916 pour l'utiliser comme agent de contrôle biologique contre certaines espèces de pucerons : en Californie en 1916, 1964 et 1965; au Connecticut, au Delaware, en Georgie, en Louisiane, au Maine au Maryland, au Mississippi, en Nouvelle-Écosse, en Ohio, en Pennsylvanie, de 1978 à 1982 et au Connecticut en 1985 (Gordon 1985; LaMana et Miller 1996; Tedders et Schaefer 1994). Ces introductions ont semblé infructueuses jusqu'en 1988 où les premiers individus ont été récoltés en Louisiane (Tedders et Schaefer 1994). Les premières apparitions de cette espèce au Québec ont été notées en 1994 dans un verger de pommiers à Frelishburg (Coderre *et al.* 1995). Depuis, elle semble s'être établie car on la retrouve dans plusieurs régions du Québec; elle a été retrouvée jusqu'au Saguenay Lac St-Jean (Lucas *et al.* Annexe A). Elle est aussi présente dans plusieurs provinces au Canada (Hagley 1999; McCorquodale 1998; Turnock *et al.* 2003; Wise *et al.* 2001). Elle a été retrouvée au Brésil (de Almeida et da Silva 2002) et en Argentine (Saini 2004). Elle a aussi été récemment introduite dans divers pays

d'Europe, où elle s'installe avec succès (voir Lucas *et al.* Annexe B; Majerus *et al.* 2006; San Martin *et al.* 2005).

2.4.1- Mécanismes possibles pour l'invasion de *Harmonia axyridis*

Au début de ce doctorat, très peu de connaissances avaient été amassées sur le succès d'invasion des coccinelles et sur le succès d'invasion de la coccinelle asiatique *H. axyridis*. Depuis le début de l'année 2001, pas moins de 100 articles sur la coccinelle asiatique ont été publiés dans les revues scientifiques. La prochaine section traitera de façon succincte des données et hypothèses qui permettraient le succès d'invasion de cette coccinelle. Des revues de littérature sur la biologie et l'écologie de cette espèce ont été effectuées par Koch (2003), Majerus *et al.* (2006) et Pervez et Omkar (2006).

Le succès d'invasion d'une espèce envahissante peut être dû à ses caractéristiques biologiques, aux caractéristiques de la communauté et de l'environnement (Shea et Chesson 2002; Shea *et al.* 2005). La coccinelle asiatique semble posséder différentes caractéristiques biologiques et des habiletés comportementales lui conférant une bonne capacité d'invasion au sein des communautés d'insectes. Toutefois, au début de ce doctorat, plusieurs informations n'étaient pas connues sur certains traits d'histoire de vie de la coccinelle asiatique au Québec et sur ses habiletés compétitrices sous différents facteurs environnementaux. Le reste du travail est divisé en trois sections, soit les caractéristiques biologiques de la coccinelle, les habiletés de compétition au sein des communautés qui pourraient expliquer la capacité d'invasion de la coccinelle asiatique, et les caractéristiques de l'environnement qui peuvent jouer sur sa capacité d'invasion.

2.4.2 Caractéristiques biologiques et traits d'histoire de vie de la coccinelle asiatique

Les adultes de la coccinelle asiatique mesurent entre 4,8 et 7,5 mm de long et 4,0 à 6,6 mm de large et les femelles sont généralement plus grosses que les mâles

(Koch 2003). Le cycle de vie holométabole de la coccinelle asiatique est semblable aux autres coccinelles aphidiphages, c'est-à-dire un stade œuf, quatre stades larvaires, un stade pupal et l'adulte (Hodek 1973). Le développement de *H. axyridis* sur différents pucerons prend entre 21 et 24 jours de l'œuf à l'adulte (Teddars et Schaefer 1994). Par exemple, Soares (2000) a montré qu'elle se développait en 22,6 jours sur le puceron de la fève *Aphis fabae* Scopoli (Coutin R. / OPIE). L'espèce de pucerons mangé et la température vont influencer le temps de développement de cette coccinelle. Le temps de développement d'une espèce envahissante peut être primordial pour son succès d'invasion (Marco *et al.* 2002). Un temps plus court pourrait lui permettre d'avoir accès aux ressources avant les autres espèces. La coccinelle maculée, *Coleomegilla maculata lengi* Timberlake, une coccinelle indigène considérée dans notre étude comme équivalent écologique, a un développement qui peut durer autour de 23,7 jours selon les conditions environnementales (Coderre 1983; Obrycki et Tauber 1978). Toutefois, le temps passé à chaque stade larvaire peut être important pour la survie, car les premiers stades larvaires peuvent être très vulnérables à la prédation (Koch 2003; Yasuda et Kimura 2001). Des temps de développement plus courts pour les premiers stades larvaires pourraient donc lui conférer un avantage durant son invasion. Peu de comparaisons du développement de la coccinelle asiatique avec des espèces natives ont cependant été effectuées. Lanzoni *et al.* (2004) a comparé le développement de la coccinelle asiatique et deux espèces natives, *A. bipunctata* et *H. variegata* en Italie. La coccinelle asiatique se développait plus lentement que les deux espèces natives et ils ont suggéré que ses caractéristiques biologiques ne semblaient pas être des facteurs expliquant son succès d'invasion. La coccinelle asiatique n'est toutefois pas présente dans leur pays et ils avaient utilisé dans leur expérience des coccinelles provenant d'élevage aux Pays-Bas (Lanzoni *et al.* 2004). La coccinelle asiatique a une durée de vie entre 30 et 90 jours en moyenne (Soares *et al.* 2001). En laboratoire, la femelle peut pondre jusqu'à 3819 œufs, avec une moyenne par jour de 25,1 œufs/jour (Hukusima et Kamei 1970). Cette fécondité, beaucoup plus élevée que

d'autres espèces de coccinelles, peut lui conférer une bonne valeur adaptative et une grande capacité d'invasion (Soares 2000).

La coccinelle asiatique présente un grand polymorphisme de coloration; plus de 100 morphes différents sont observés chez cette espèce, qui sont héréditaires et associés à une série d'allèles multiples (Hodek et Honěk 1996). La tête peut être noire, jaune ou noire avec des barres jaunes (voir Koch 2003). Le pronotum est jaunâtre avec des marques noires au centre, qui forment un M, deux lignes courbées, quatre points noirs ou un trapèze noir (Chapin et Brou 1991). La coloration des élytres varie du jaune-orange à rouge avec aucun à 19 points noirs, ou noires avec des points rouges. Les morphes noirs à points rouges ont été observés dans l'État d'Oregon et dans le Nord-Ouest des États-Unis (Krafsur *et al.* 1997). Un individu noir a été récolté au Québec (Chouinard, communication personnelle). Ce grand polymorphisme peut être dû à une grande variabilité génétique, caractéristique importante pour la capacité d'envahir et de s'établir dans des environnements changeants (Soares *et al.* 2001). Krafsur *et al.* (1997) ont effectué des analyses du flot génétique sur différentes populations de la coccinelle asiatique en Amérique du Nord et n'ont pas découvert de sélection ou d'adaptation régionale à la suite de sa dispersion. Récemment, Krafsur *et al.* (2005) ont démontré que la diversité génétique de plusieurs espèces de coccinelles indigènes (*C. maculata*, *C. novemnotata*, *H. convergens*, *Hippodamia parenthesis* (Say), *Hippodamia tredecimpunctata tibialis* (Say), *Cycloneda munda* (Say)) et envahissantes (*H. axyridis*, *A. bipunctata*, *C. septempunctata*, *P. quatuordecimpunctata*, *H. variegata*, *Eriopis connexa* (Germar) et *Scymnus frontalis* (Fabricius)) était similaire, n'appuyant donc pas l'hypothèse sur la relation entre une plus grande diversité génétique et le succès de colonisation. Grill *et al.* (1997) ont démontré que la variation génétique de *H. axyridis* pouvait cependant lui permettre des changements adaptatifs dans les taux de développement et dans la taille. Cette variabilité génétique pourrait donc lui permettre un meilleur

succès, mais il faut encore effectuer des études à plus long terme afin de mesurer la sélection à travers le temps.

La coccinelle asiatique est polyphage, s'attaquant à plus de 30 espèces de pucerons, mangeant des tétranyques, des coccides, des psylles, des chrysomèles, des charançons, des lépidoptères, du pollen et du nectar (voir Koch 2003; Lucas *et al.* Annexe B; Tableau 1). La coccinelle asiatique possède une bonne efficacité de recherche de proies (Osawa 2000; With *et al.* 2002), ce qui lui permet de trouver ses proies dans divers environnements. L'efficacité de recherche et d'attaque d'une espèce (les différents paramètres du temps de recherche, d'attaque, de manipulation et d'ingestion) peut être un facteur déterminant pour expliquer la capacité d'invasion de *H. axyridis* (Dixon 2000). Si elle est meilleure à détecter la proie, à l'attaquer et à la manger, cela pourrait expliquer sa supériorité en tant que compétitrice. Sa grande voracité, elle peut manger plus de 80 pucerons par jour (Soares *et al.* 2001), peut lui conférer un avantage en compétition par exploitation. Sa capacité à convertir la biomasse ingérée en biomasse corporelle, pourrait aussi être une caractéristique favorisant l'invasion de la coccinelle asiatique. Selon Schanderl *et al.* (1985), *H. axyridis* a une efficacité de conversion (poids adulte (μg)/consommation des larves (μg)) de 0,29, tandis que *C. septempunctata* a une efficacité de 0,13 (Formisoh et Wilde 1993). La coccinelle asiatique convertit donc plus efficacement les proies en biomasse, ce qui peut lui donner un avantage lors de l'invasion d'un nouveau milieu car son développement peut être plus rapide et sa fécondité et sa fertilité plus grande que les autres espèces. Très peu de comparaisons ont été effectuées sur les taux de conversion des différentes espèces de coccinelles et cette caractéristique pourrait expliquer en partie la capacité d'invasion de la coccinelle asiatique.

Ainsi, certaines caractéristiques de la coccinelle asiatique, telles son développement, sa fécondité, sa variabilité phénotypique et son efficacité de prédation pourraient lui permettre une meilleure capacité d'invasion. Malgré ces informations, des questions restaient sans réponse, tant au niveau du temps de

développement ou de l'efficacité de prédation des différents stades larvaires de cette espèce.

2.4.3. Les caractéristiques des communautés et l'invasion de la coccinelle asiatique

Les guildes d'insectes aphidiphages (qui se nourrissent de pucerons) sont constituées de coccinelles, de carabes, de chrysopes, d'hémérobes, de syrphes, de cécidomyies, d'hémiptères, tels que les nabides, les réduviides, les mirides, les anthocorides et les lygaeides, ainsi que des araignées (voir Lucas 2005). De nombreuses interactions sont possibles au sein des communautés aphidiphages, que ce soit par compétition par exploitation, par interférence, particulièrement par la prédation intragilde ou par la compétition apparente (Lucas 2005).

Il est difficile de mesurer la compétition par exploitation. Evans (1991) a tenté de démontrer un effet de la compétition par exploitation sur le gain en poids de larves des coccinelles *H. convergens*, *Hippodamia sinuata* Mulsant et *C. septempunctata* lorsque mises ensembles ou seules à faible quantité de nourriture, mais il n'y avait pas d'effet de la présence d'un compétiteur sur aucune des espèces. La compétition par interférence semblait plus forte dans ce système, probablement à cause de leur taille semblable et de leur capacité de recherche de proies similaires. Dans une expérience de compétition interspécifique entre la coccinelle *C. maculata* et *C. septempunctata* en cage en champ, Obrycki *et al.* (1998b) ont mis en évidence un effet de la compétition par exploitation sur la coccinelle à sept points. À la fin de l'été, *C. septempunctata* avait une survie nulle dans les cages de faible densité de proies en présence de *C. maculata*. La coccinelle maculée semble donc être une meilleure compétitrice par exploitation car elle survit à faible densité de proies. Dans une expérience sur pommier en laboratoire, Lucas *et al.* (2002) ont montré qu'il n'y avait pas une forte compétition par exploitation de pucerons entre la coccinelle asiatique et la coccinelle à sept points. Dans les combinaisons hétérospécifiques, les

adultes des deux espèces ont consommé le nombre de pucerons qu'ils auraient consommé étant seuls. Michaud (2002) a démontré que la coccinelle asiatique était plus vorace, plus fertile et féconde que *C. sanguinea*, ce qui lui permettait de la supplanter directement pour la ressource. Aucune expérience n'a été effectuée entre la coccinelle maculée et la coccinelle asiatique pour évaluer les effets de la compétition par exploitation entre ces deux espèces. Les expériences de Obrycki *et al.* (1998b) suggèrent que la coccinelle maculée est meilleure en compétition par exploitation que la coccinelle à sept points, car elle peut survivre avec peu de nourriture. De plus, Persson (1985) suppose que les plus grosses espèces sont meilleures en compétition par interférence et que les petites sont meilleures en compétition par exploitation. La coccinelle maculée pourrait donc être meilleure en compétition par exploitation que la coccinelle asiatique.

Il semble que la coccinelle asiatique soit plus impliquée dans la compétition par interférence que dans la compétition par exploitation (Lucas *et al.* 2002; Lucas *et al.* Annexe B; Yasuda et Kimura 2001). Différentes études ont montré que la coccinelle asiatique est une bonne compétitrice du fait de sa grande taille et de son agressivité (Cottrell et Yeagan 1998c; Hironori et Katsuhiko 1997; Yasuda et Shinya 1997; Yasuda et Ohnuma 1999; Yasuda *et al.* 2001; 2004). Des études dans le nord du Japon ont suggéré que *H. axyridis* était dominante par la prédation de ses larves sur les larves de *C. septempunctata* quand les pucerons deviennent peu abondants (Hironori et Katsuhiko 1997; Yasuda et Shinya 1997). Plusieurs remplacements et diminutions marquées des populations de *C. septempunctata* dans les écosystèmes agricoles et naturels dans différentes régions des États-Unis ont été notés à la suite de l'invasion de la coccinelle asiatique (Brown 2003; Brown et Miller 1998; Reitz et Trumble 2002). Des diminutions de populations de *Brachiacantha ursina* (F.), *C. munda* et *Chilocorus stigma* (Say) ont aussi été notées après l'établissement de la coccinelle asiatique aux États-Unis (Colunga-Garcia et Gage 1998). La prédation intragilde de *H. axyridis* sur les autres espèces de coccinelles serait une des raisons

de ces déplacements (Hironori et Katsuhiko 1997; Lucas *et al.* Annexe B, Tableau 2; Reitz et Trumble 2002). Cottrell et Yeargan (1998c) ont mesuré la prédation intragilde en laboratoire entre *H. axyridis* et *C. maculata*. Ils ont montré que *H. axyridis* se développait bien sur des œufs ou des larves de *C. maculata* et que dans presque toutes les combinaisons entre 2^{ème} et 4^{ème} stade larvaire, il y avait une prédation intragilde asymétrique en faveur de *H. axyridis*. Ils ont aussi observé en champ des coccinelles asiatiques (adultes et larves) mangeant des œufs ou des larves de la coccinelle maculée dans le maïs sucré (Cottrell et Yeargan 1998a, b). Lucas *et al.* (Annexe B; Tableau 2) ont dénombré 16 études dans lesquelles la coccinelle asiatique fait de la prédation intragilde sur d'autres espèces. Cette asymétrie dans les interactions avec les autres espèces au sein des communautés aphidiphages pourrait donc lui permettre d'envahir les nouveaux milieux avec succès et expliquerait sa dominance dans divers écosystèmes (Lucas *et al.* 2002; Lucas *et al.* Annexe A, Annexe B; Yasuda et Kimura 2001).

Divers facteurs peuvent influencer l'intensité de la prédation intragilde (Lucas 2005). Par exemple, la différence de taille entre le prédateur et la proie intragilde peut influencer grandement l'issue de l'attaque. L'intensité de la prédation intragilde devrait augmenter lorsque la différence en taille entre le prédateur et la proie intragilde augmente (Félix et Soares 2004; Lucas 2005; Snyder *et al.* 2004). Cependant, ce n'est pas ce qui a été retrouvé entre la coccinelle asiatique et la coccinelle indigène *C. undecimpunctata* : la coccinelle asiatique avait une forte intensité de prédation intragilde même avec une faible différence en taille avec la coccinelle indigène (Félix et Soares 2004, voir aussi Yasuda *et al.* 2004). Elle semble donc un prédateur très efficace même avec de faibles différences en taille. Dixon (2000) lui a d'ailleurs donné le rang de *top*-prédateur, en se basant sur sa grande capacité de prédation intragilde et sur l'hypothèse que ses œufs sont protégés de façon chimique et que ses larves, avec leurs épines et leurs larges mandibules,

devraient être mieux protégées contre la prédation intraguilde que les autres espèces de coccinelles.

Le cannibalisme, ou prédation intraspécifique, est aussi classé parmi la compétition par interférence. Le cannibalisme est courant entre les prédateurs arthropodes (Schellhorn et Andow 1999), spécialement chez les coccinelles (Agarwala et Dixon 1992; Hemptinne *et al.* 2000; Mills 1982; Osawa 1989; Schellhorn et Andow 1999; Snyder *et al.* 2000), car il apporte un bénéfice nutritionnel et une diminution de la compétition (Burgio *et al.* 2002; Osawa 1993; 2000; Polis 1981). Les larves et les adultes de *H. axyridis* sont très cannibales (Osawa 1989; Hodek et Honěk 1996; Snyder *et al.* 2000; Burgio *et al.* 2002). Jusqu'à 30% des œufs de la coccinelle asiatique peuvent être consommées par des conspécifiques (Osawa 1993). Osawa (1993; 2000) suppose que le cannibalisme des œufs chez cette espèce lui permet de soutenir des populations dans des environnements changeants où les ressources fluctuent, ce qui lui permettrait ainsi d'envahir des habitats avec peu de ressources. Hoogendoorn et Heimpel (2004) ont mesuré les interactions en cages en champ de maïs entre des larves de 1^{er} stade de la coccinelle asiatique et de la coccinelle maculée. Après une semaine, il n'y avait pas d'impact de la présence de la coccinelle asiatique sur la coccinelle maculée, ce qu'ils ont attribué au fait que la coccinelle asiatique a un taux de cannibalisme assez élevé, ce qui diminuerait la pression de prédation sur les larves de la coccinelle maculée. Ce cannibalisme pourrait aussi permettre une certaine coexistence avec les espèces indigènes, une hypothèse qui reste à vérifier.

Dans le cas de la compétition apparente, il semble que la présence de la coccinelle asiatique aurait eu un effet positif sur les populations de la coccinelle maculée (Hoogendoorn et Heimpel 2002). Le parasitoïde *Dinocampus coccinellae* Schrank semble avoir une préférence à attaquer la coccinelle asiatique, ce qui pourrait réduire les attaques sur la coccinelle maculée (Firlej, thèse de doctorat). Toutefois, aucun parasitoïde n'émerge des coccinelles asiatiques parasitées (Firlej *et al.* 2005); il

semblerait que la compétition apparente n'influence pas l'invasion de la coccinelle asiatique.

Il semble que la coccinelle asiatique soit peu attaquée par les ennemis naturels. Lorsqu'elle est mangée, c'est en général parce qu'elle est de plus petite taille (e.g. Cottrell et Yeorgan 1998c). L'expérience en laboratoire de Yasuda et Kimura (2001) a démontré que la coccinelle asiatique était moins affectée par la présence de l'araignée-crabe *Misumenops tricuspidatus* (Fabricius) que la coccinelle à sept points. Aucune larve de 2^{ème}, 3^{ème} ou 4^{ème} stade larvaire n'ont été consommées par l'araignée et le développement de la coccinelle était ralenti seulement au 2^{ème} stade larvaire. Les larves de la coccinelle asiatique semblaient mieux se défendre contre l'araignée que celles de la coccinelle à sept points. Yasuda *et al.* (2001) attribuent son succès de prédation au fait qu'elle a des taux d'attaques plus élevés et une plus grande habileté de fuite que la coccinelle à sept points. Toutefois, DeClercq *et al.* (2003) ont démontré que la coccinelle asiatique était généralement attaquée et mangée par le pentatomide *Podisus maculiventris* (Say). Plusieurs espèces de parasitoïdes et de champignons entomopathogènes, tels que *D. coccinellae*, *Strongygaster triangulifera* (Loew) (Diptera: Tachinidae) ou *Beauveria bassiana* (Balsamo) s'attaquent aux coccinelles (Ceryngier 2000; Cottrell et Shapiro-Illan 2003; Firlej *et al.* 2005; Katsoyannos et Alinyazee 1998). Malgré la présence du parasitoïde *D. coccinellae* au Québec, le taux de parasitisme de cette espèce est de 1 à 5%, toutefois sans émergence de parasitoïde (Firlej *et al.* 2005). Le parasitoïde *S. triangulifera*, infecte la coccinelle asiatique entre 1 et 31% aux États-Unis (Katsoyannos et Aliniyazee 1998; LaMana et Miller 1996; Nalepa *et al.* 1996) et pourrait être présent dans nos régions (O'Hara et Wood, 2004), mais aucune coccinelle asiatique n'a été retrouvée infectée par celui-ci (Firlej, communication personnelle). Des études récentes ont aussi montré que le champignon entomopathogène *B. bassiana*, qui s'attaque aux coccinelles durant l'hibernation, ne causait pas de mortalité chez la coccinelle asiatique (Cottrell et Shapiro-Illan 2003). La coccinelle asiatique semble aussi peu susceptible à des

nématodes entomopathogènes, ce qui n'était pas le cas pour la coccinelle à sept points (Shapiro-Illan et Cottrell 2005). Des observations dans la zone Paléarctique montre que la coccinelle asiatique était mangée par 8 espèces d'oiseaux (Netschayev et Kuznetsov 1973 dans Hodek et Honěk 1996), mais aucune observation n'a été effectuée au Québec. Elle semble donc libre d'ennemis naturels dans nos régions, ce qui viendrait appuyer l'*enemy release hypothesis* (Keane et Crawley 2002), où la coccinelle asiatique serait moins attaquée que les ennemis naturels indigènes, ce qui expliquerait en partie son succès d'invasion.

Le succès d'invasion de la coccinelle asiatique au sein des communautés aphidiphages pourrait donc être dû à sa grande capacité de compétition, principalement par la prédation intraguilde et par le peu d'ennemis naturels efficaces présents dans nos régions. Malgré le grand nombre d'études sur la prédation intraguilde de la coccinelle asiatique sur d'autres espèces, très peu d'études ont été effectuées pour évaluer la prédation intraguilde entre tous les stades larvaires. Il serait intéressant de vérifier si les premiers stades larvaires et les œufs sont protégés de la prédation intraguilde, ce qui appuierait le statut de *top*-prédateur. Dans le cas des ennemis naturels, les travaux de A. Firlej au sein de notre laboratoire ont couvert l'étude du parasitisme par *D. coccinellae*.

2.4.4. Les caractéristiques de l'environnement et l'invasion de la coccinelle asiatique

Les caractéristiques abiotiques et biotiques de l'environnement, les perturbations, la fragmentation de l'habitat et autres caractéristiques du milieu peuvent affecter le succès d'invasion d'une espèce envahissante (Mack *et al.* 2000; Von Holle et Simberloff 2005). Peu de choses sont connues sur les caractéristiques de l'environnement qui sont favorables ou qui amènent une résistance à l'invasion de la coccinelle asiatique. La capacité de dispersion de la coccinelle asiatique semble très grande. La colonisation de l'Amérique du Nord s'est effectuée très rapidement. En

seulement deux ans, la coccinelle s'est dispersée à travers l'État de Georgie (149 977 km²) et dans les états adjacents de Floride et Caroline du Sud aux États-Unis (1994) (Majerus *et al.* 2006). L'étude de McCorquodale (1998) fait mention d'une expansion moyenne par année de la coccinelle asiatique de 442 km, tandis que la coccinelle à 7 points aurait une expansion de 108 km/an et la coccinelle à 14 points de 31 km/an. Ces taux d'expansions peuvent toutefois être surestimés du fait des introductions intentionnelles des coccinelles comme agents de lutte biologique (McCorquodale 1998). Toutefois, ils donnent une idée de l'expansion explosive de la coccinelle asiatique en Amérique du Nord. Au Québec, la coccinelle s'est dispersée dans toutes les régions du Québec depuis 1994, ayant été retrouvée jusqu'à Dolbeau-Mistassini, au Lac St-Jean (Labrie, observation personnelle). Cette capacité de dispersion dans divers environnements serait une des caractéristiques lui permettant son grand succès d'invasion.

La coccinelle asiatique a été identifiée comme une espèce arboricole qui se retrouve dans les vergers, les forêts et la végétation de fin de succession (Brown et Miller 1998; Chapin et Brou 1991; Coderre *et al.* 1995; Hodek 1973; LaMana et Miller 1996; McClure 1986; Tedders et Schaefer 1994). Cependant, on la retrouve dans la plupart des écosystèmes agricoles, où elle s'y nourrit et s'y reproduit (LaMana et Miller 1996; Musser et Shelton 2003; Nault et Kennedy 2003; Park et Obrycki 2004; voir Lucas *et al.* Annexe A). La coccinelle asiatique est devenue la coccinelle dominante en seulement 4 ans dans les habitats observés au Michigan (Colunga-Garcia et Gage 1998). Au Québec, la coccinelle est aussi devenue dominante dans plusieurs cultures pérennes et annuelles (Lucas *et al.* Annexe A). Une étude récente a mesuré l'effet de la fragmentation en milieu agricole sur la capacité à trouver les pucerons chez la coccinelle asiatique et la coccinelle maculée (With *et al.* 2002). La coccinelle asiatique montrait une meilleure efficacité de recherche des proies dans un milieu fragmenté comparé à la coccinelle maculée dans des parcelles de trèfles. Cette nature eurytopique, qui lui confère une capacité à exploiter les

ressources de différents habitats, lui permettrait donc de mieux survivre et se reproduire dans l'environnement qu'elle envahit.

Le climat est un facteur abiotique qui peut influencer grandement la survie des insectes (Bale 1991). Par exemple, la survie hivernale de la coccinelle maculée dans les régions plus nordique de l'Amérique du Nord peut osciller entre 3 à 57% (Benton et Crump 1979; Coderre *et al.* 1995; Jean *et al.* 1990; Wright et Laing 1982). La coccinelle asiatique semble montrer une bonne résistance à l'hiver dans son pays d'origine (Iablokoff-Khnozorian 1982). En automne tardif, les adultes émigrent sur des sites d'hibernation, habituellement des sites en hauteur, isolés, et relativement secs, où ils s'agrègent pour survivre à l'hiver (Obata 1986; Obata *et al.* 1986; Nalepa *et al.* 2005; Sakurai *et al.* 1992). La coccinelle asiatique accumule du glycogène, des lipides et du myoinositol dans l'hémolymph, ce qui lui permet de survivre quelques jours à des températures de -15°C (Koch *et al.* 2004; Sakurai *et al.* 1992; Watanabe 2002). Par contre elle ne survit pas à des températures sous -20°C au Japon (Watanabe 2002). McClure (1987) a étudié la survie hivernale de la coccinelle asiatique dans des cages au Connecticut, et a rapporté une survie de 10% après le premier hiver et de 0% le deuxième. Il a suggéré que les conditions climatiques durant l'hiver serait un facteur très important pour réguler les populations de cette espèce envahissante. Cependant, en Amérique du Nord, la coccinelle asiatique hiberne à l'intérieur des maisons, où elle peut constituer une nuisance pour les humains (Hagley 1999; Huelsman *et al.* 2001; Kidd and Nalepa 1995; Kovach 2004; LaMana and Miller 1996; Lucas *et al.* Annexe B; McCutcheon and Scott unpubl; Nalepa *et al.* 1996; Riddick *et al.* 2000; 2004; Yarbrough *et al.* 1999). Une expérience récente a démontré que le point de surfusion (température à laquelle les tissus gèlent) de cette espèce se situe entre -12 et -16°C , et que sa capacité à survivre à l'hiver serait liée à la qualité des sites d'hibernation plutôt qu'à sa capacité à augmenter sa tolérance au froid (Koch *et al.* 2004). Cependant, aucune étude n'a été effectuée sur sa capacité d'hibernation au Québec et au Canada.

La quantité de ressources du milieu pourrait aussi affecter la capacité d'invasion de la coccinelle asiatique (Marco *et al.* 2002; Tilman 1999). Ainsi, si elle est moins bonne en compétition par exploitation, elle ne devrait pas réussir à survivre quand il y a peu de ressources, tandis qu'à forte quantité de ressources, elle devrait compétitionner avec les autres espèces par la prédation intragilde. L'étude récente de Hoogendoorn et Heimpel (2004) a mesuré l'effet d'une faible et forte quantité de ressources sur la survie de larves de 1^{er} stade de la coccinelle asiatique et maculée durant 7 jours. Il n'y a pas eu d'effets sur la survie ou le gain en poids des larves selon la quantité de nourriture ou la présence d'un compétiteur. Ces résultats sont cependant partiels car l'expérience n'a été effectuée que sur des larves de 1^{er} stade et seulement durant une semaine. Des expériences sont encore à effectuer pour mieux comprendre l'influence des ressources sur la capacité d'invasion de la coccinelle asiatique et sa coexistence avec d'autres espèces.

2.5. La coccinelle maculée *C. maculata*

Tout au long de ce doctorat, nous avons choisi de comparer les caractéristiques biologiques, les interactions, la survie hivernale et l'effet de la quantité de ressources sur la coccinelle asiatique et la coccinelle maculée *C. maculata*. La coccinelle maculée est une des plus grosses espèces de coccinelle native au Québec, présentant un temps de développement similaire à la coccinelle asiatique, 23 à 25 jours pour la coccinelle maculée (Coderre 1983 ; Obrycki et Tauber 1978), contre 21 à 24 jours pour la coccinelle asiatique (Soares 2000). Sa fécondité est toutefois moindre, une femelle pouvant pondre 650 œufs dans sa vie (Coderre 1983), contre un maximum de 3800 pour la coccinelle asiatique (Hodek 1973). La coccinelle maculée est aussi une espèce eurytopique, on la retrouve dans diverses cultures annuelles et pérennes ainsi qu'en milieu naturel. Elle est polyphage, se nourrissant de pucerons, de pyrale du maïs, du doryphore de la pomme de terre *Leptinotarsa decemlineata* (Say), d'œufs de lépidoptères ou de pollen (Coderre *et al.* 1987 ; Giroux *et al.* 1995 ; Hodek *et al.* 1978 ; Warren et Tadic 1967). Cette nature

eurytopique et sa plus faible demande de nourriture faciliterait sa survie (Obrycki *et al.* 1998b). Elle serait donc une meilleure compétitrice par exploitation que les plus grosses espèces comme la coccinelle à sept points. Wise *et al.* (2001) ont récemment observé la coccinelle asiatique ainsi que la coccinelle maculée dans la province du Manitoba au Canada. Ces deux espèces n'avaient jamais été répertoriées auparavant dans cette région, indiquant que la coccinelle maculée a aussi certaines capacités d'invasion. Ces différentes caractéristiques similaires entre l'espèce indigène et envahissante nous permettait donc d'évaluer le succès d'invasion de la coccinelle asiatique en la comparant à cette espèce indigène.

2.6. Objectifs et hypothèses

Ainsi les caractéristiques biologiques de l'espèce, les habiletés compétitrices de la coccinelle au sein des communautés aphidiphages ainsi que l'influence des caractéristiques de l'environnement abiotique telles que la survie durant l'hiver québécois et biotique comme la quantité des ressources ont été prises en compte durant ce doctorat. La coccinelle asiatique a été comparée tout au long de ce doctorat à une espèce indigène, la coccinelle maculée *C. maculata*, qui est un équivalent écologique de la coccinelle asiatique et utilise les ressources de façon similaire au niveau spatial et temporel (Labrie *et al.* données non publiées; Musser et Shelton 2003; Nault et Kennedy 2003; Park et Obrycki 2004).

Au chapitre 1, certaines caractéristiques biologiques de la coccinelle asiatique ont été comparées avec celles de la coccinelle maculée. Nous avons formulé l'hypothèse que la coccinelle asiatique présentait un développement plus rapide et des comportements d'alimentation plus efficaces que la coccinelle maculée.

Au chapitre 2, la prédation intragilde a été mesurée entre la coccinelle asiatique, la coccinelle maculée et entre ces deux espèces et une autre espèce envahissante, la coccinelle à 14 points. L'hypothèse testée était que la coccinelle asiatique était un meilleur prédateur intragilde que les deux autres espèces. Nous avons aussi testé l'hypothèse que la coccinelle asiatique induirait des effets indirects sur la perte de poids de la coccinelle maculée.

Le chapitre 3 évalue la survie de la coccinelle asiatique au regard d'une caractéristique environnementale abiotique, la température durant l'hiver québécois. Nous avons formulé l'hypothèse que la coccinelle asiatique ne pouvait survivre aux températures sous -15°C que nous retrouvons durant l'hiver au Québec, et que la survie de la coccinelle serait possible seulement dans les maisons.

Le chapitre 4 évalue l'influence d'une caractéristique environnementale biotique, l'abondance des ressources, qui peut avoir un impact sur les variables de

population de la coccinelle asiatique ainsi que sur la coexistence avec la coccinelle maculée. Nous avons formulé une première hypothèse selon laquelle la coccinelle asiatique ne pourrait survivre sous de faibles quantités de ressources. Nous avons formulé une deuxième hypothèse selon laquelle la coccinelle asiatique ne pourrait survivre en présence de la coccinelle maculée à de faibles quantités de ressource, que la coccinelle maculée ne pourrait survivre à de fortes quantités de ressource, dû à la forte pression de prédation par la coccinelle asiatique et que la coexistence serait possible à des quantités de ressource intermédiaires.

CHAPITRE I

CAN DEVELOPMENTAL AND BEHAVIORAL CHARACTERISTICS OF THE MULTICOLORED ASIAN LADY BEETLE *HARMONIA AXYRIDIS* EXPLAIN ITS INVASIVE SUCCESS?

I.1 ABSTRACT

Major impacts of biological invasions are widely recognized and underscore the need to understand the relation between life-history traits of invasive species and the invasion process. Growth of juveniles and adult survival of invasive species are key factors in invasion process. Life-history traits that increase juvenile fitness including increased rates of development and behavioral characteristics that facilitate competitive success such as increased predator efficiency and foraging ability may explain invasiveness of a species. Invasion of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in North America provides an opportunity to investigate life-history traits of juveniles of an invasive species. Here, we evaluate both developmental and behavioral traits that may explain the success of *H. axyridis* by comparing it to an ecologically similar indigenous species *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae). Three points may contribute to the invasiveness of *H. axyridis*. First, development of *H. axyridis* was faster during the 2nd larval instar than *C. maculata*, a characteristic that may reduce vulnerability at young instars. Second, *H. axyridis* reached the 4th instar more rapidly than *C. maculata*. The 4th instar of *H. axyridis* was also characterized by higher predation efficiency with increased voracity, lethal contact and search efficiency of pea aphids *Acyrtosiphon pisum*. Finally, surprisingly, a 5th larval instar occurred in 33% of the individuals of *H. axyridis* and was characterized by the same developmental time, but with increased voracity and weight gain compared to 4th larval instars, suggesting an increased fitness of these individuals. These developmental characteristics coupled with increased predation efficiency and behavioral characteristics enhanced the juvenile growth and predatory abilities of this species and may contribute to the invasive ability of *H. axyridis*.

Key words: *Coleomegilla maculata lengi*, developmental characteristics, foraging behavior, *Harmonia axyridis*, invasive species, invasiveness, predation efficiency

I.2 INTRODUCTION

Biological invasions are having major ecosystem impacts and are thought to be the second leading cause of biodiversity loss (Pimentel *et al.* 2000; Vitousek *et al.* 1996). The need to limit the impact of nonindigenous species on natural communities has generated many recent experimental studies (Kolar and Lodge 2001; Keane and Crawley 2002; Snyder *et al.* 2004). Many biological and environmental factors could contribute to the invasiveness of species (Marco *et al.* 2002). It is thought that life-history traits like increased developmental rate, fecundity and fertility are important for successful invasion and establishment (Sakai *et al.* 2001; Shea and Chesson 2002; Marco *et al.* 2002; Lanzoni *et al.* 2004) and their knowledge are of basic importance to develop a better understanding of interspecific interactions among exotic and native species (Krijger *et al.* 2001; Lanzoni *et al.* 2004). The key factor in invasion process is juvenile growth, as safe growth in these vulnerable stages can ensure high population growth in the new environment (Marco *et al.* 2002). Release from natural enemies and parasites (Kimberling 2004; Hierro *et al.* 2005), resources productivity of the new environment (Marco *et al.* 2002) and increased opportunities for colonization caused by anthropogenic disturbances (Mack *et al.* 2000) can also increase the invasibility of a species. Ecologists are limited in their ability to identify likely successful invaders prior to establishment (Snyder *et al.* 2004). Hence, there is a need to understand the underlying biological mechanisms explaining invader success (Keane and Crawley 2002; Shea and Chesson 2002; Kimberling 2004).

The multicolored Asian lady beetle, *Harmonia axyridis* Pallas, has been released many times in North America since 1916 as a classical biological control agent against aphids (Gordon 1985). The first established population was reported in Louisiana in 1988 (Chapin and Brou 1991) and it spread rapidly across North America the following years (Teddars and Schaefer 1994; Colunga-Garcia and Gage 1998). This coccinellid appeared in Canada in 1994 (Coderre *et al.* 1995) and is now widely present in many ecosystems (Lucas *et al.* 2002; Lucas *et al.* Annexe A;

Turnock *et al.* 2003). This species is polyphagous and eurytopic (Iablokoff-Khnzorian 1982; Tedders and Schaefer 1994; Hodek and Honěk 1996; Lucas *et al.* 1997a; Koch 2003). *Harmonia axyridis* is a strong intraguild predator of the other coccinellid species (Cottrell and Yeargan 1998; Yasuda and Ohnuma 1999; Yasuda *et al.* 2001; Burgio *et al.* 2002; Cottrell 2004; Félix and Soares 2004; Snyder *et al.* 2004), possibly of chrysopids (Brown 2003), and some studies supposed that it is displacing competitively *Coccinella septempunctata* L. in mid-Western USA (Brown and Miller 1998; Reitz and Trumble 2002; Brown 2003), *Coccinella transversoguttata* Brown in Maine (USA) (Alyokhin and Sewell 2004) and *Cycloneda sanguinea* (L.) in Florida (USA) (Michaud 2002). Intraguild predation (IGP) has been reported between *H. axyridis* and the native *Coleomegilla maculata lengi* Timberlake in laboratory and in field, with asymmetric interaction in favor of *H. axyridis* (Cottrell and Yeargan 1998; Cottrell 2004); greater impact of the exotic species can be expected in the field on native species (Yasuda *et al.* 2001; Cottrell 2004).

Harmonia axyridis dominate aphidophagous guilds in some agricultural ecosystems in part due to high fecundity (Iablokoff-Khnzorian 1982), large body size (Michaud 2002), polyphagous feeding (Koch 2003), aggressive behavior (Cottrell and Yeargan 1998; Yasuda and Ohnuma 1999; Yasuda *et al.* 2001; Cottrell 2004; Félix and Soares 2004; Snyder *et al.* 2004), high mobility (Osawa 2000; With *et al.* 2002) and low susceptibility to pathogens (Hoogendoorn and Heimpel 2002; Cottrell and Shapiro-Ilan 2003; Firlej *et al.* 2005;). Rapid juvenile development of *H. axyridis* relative to indigenous species could be another characteristic of invasiveness of this species (Lanzoni *et al.* 2004).

Another attribute that may determine predator success in agricultural ecosystems is their searching strategies (Lanzoni *et al.* 2004; Munyaneza and Obrycki 1998b; Osawa 2000). The searching strategies resulting in the most successful prey capture can favor individuals in a species, determine the functional response and

influence the numerical and developmental responses of a species (Munyaneza and Obrycki 1998a; Dixon 2000). In this regard, it is supposed that an invasive species will have better searching strategies that result in higher predation efficiency than indigenous ones (Kimberling 2004).

The objective of this study was to evaluate some developmental and behavioral characteristics that could explain this invasion success in Canadian ecosystems. We chose to compare the invasive species *H. axyridis* with the native *C. maculata* because they share many similar characteristics: they belong to the same tribe Coccinellini (Iablokoff-Khnzorian 1982), they are polyphagous (Hodek and Honěk 1996), they overlap spatially and temporally in some crops (sweet corn: Musser and Shelton 2003; corn: Hoogendoorn and Heimpel 2004; Labrie *et al.* in preparation) and the comparison with an indigenous species can allow us to point out which juvenile characteristics may explain invasiveness of *H. axyridis*. We hypothesized that (1) the preimaginal developmental time of *H. axyridis* will be shorter than *C. maculata* and (2) the predation efficiency will be greater for *H. axyridis* than *C. maculata*.

I.3 MATERIAL AND METHODS

Insects

Harmonia axyridis were collected in agricultural fields around Montreal, Quebec (74°00' W, 45°21' N) in June 2003. *Coleomegilla maculata* were collected at overwintering sites near St-Hyacinthe, Quebec (72°56' W, 45°39' N) in April 2003. Adults were maintained in the laboratory in muslin cages at constant temperature (24 °C) photoperiod (16L : 8D) and relative humidity (RH : 60–75%). Both species were fed a mixed diet of pea aphids, *Acyrtosiphon pisum* Harris, a liver based artificial diet (Firlej *et al.* in preparation) and eggs of *Ephestia kuehniella* Zeller (Lepidoptera : Pyralidae). The pea aphid *A. pisum* used in development experiment were maintained on broadbean plants *Vicia faba* L. under the same conditions.

Preimaginal development

Eggs of each coccinellid species were removed from cages and maintained in control chambers between 23 and 25 °C, 16L:8D, 60–75% RH until eclosion. One 1st instar larvae of each species was placed individually on one broadbean plant encaged in a transparent plastic container of 30 cm height and 10 cm width with muslin openings. This set-up was repeated 15 times for each species. All cages were maintained under identical conditions. The number of *A. pisum* offered to predator larvae depended on the developmental stage of coccinellid (Soares *et al.* 2001). Based on preliminary tests we offered to coccinellid larvae: 10 individual aphids for 1st instar, 20 for 2nd, 30 for 3rd, 40 for 4th, 60 for 5th (when present). Aphids were deposited daily on each plant. Gravid female aphids were not used because of their capacity to reproduce and increase aphid density. Aphids of 2nd or 3rd instar were added daily in order to keep the density constant. Aphids were weighed to assess biomass availability for coccinellids. Coccinellid larvae were weighed each day before adding new aphids. The presence of exuviae was noted and examined to determine the larval instar. Pre-imaginal developmental time was calculated in days

from the date of hatching to adult emergence. Developmental time was also recorded for each predator larvae instar separately. Survival was determined as the proportion of larvae that emerged successfully as adults. Adult emergence (AE) and growth index (GI) were calculated (Table 1). Survival, growth index and adult emergence of both species were compared with χ^2 -test. We compared developmental time between species for each larval instar using ANOVA. Squared root transformations were used on developmental time to normalize data distribution (Sokal and Rohlf 1995). All statistical analyses were performed with JMP 5.0® (SAS Institute).

Predation efficiency

The number of aphids eaten/day by each coccinellid was counted and the voracity (V) was determined (Lucas *et al.* 1998) (Table 1). No correction of the voracity were made with a control consisting of a plant without predators because mortality of aphids was easily determined as consumed by coccinellids or desiccated at the bottom of the plant. Partially consumed aphids were not used to calculate voracity. Relative weight gain for total preimaginal development and the preimaginal relative growth rate (RGR) for each larval instar were calculated (Table 1). Weights of aphids and predator larvae permitted calculation of conversion efficiency (CE) that evaluated the efficiency of food assimilation of each species (Table 1).

Voracity, relative weight gain, RGR and CE were compared between larval instars of the two species with ANOVAs (Sokal and Rohlf 1995). Squared root transformation was used on voracity and CE to normalize data distribution (Sokal and Rohlf 1995).

Foraging behavior

Foraging behavior of each individual of the two species was observed 24 h after each molt. Observations were done over 20 min with the Software Observer 2.0 (Noldus Information Technology b.v. 1989, 1990) and the frequency and duration of the following behaviors were noted:

- Resting: Predators remain stationary, but not feeding.
- Extensive searching: Predators walk in fast linear movements between prey patches (Dixon 1959; Ettifouri and Ferran 1993). Predators shift from extensive search into handling mode upon encountering a prey (Rosenheim and Corbett 2003).
- Intensive searching: Predators walk in slow and sinuous movements (Ettifouri and Ferran 1993). This represents the local search that foraging predators often express once within a patch of prey (Rosenheim and Corbett 2003).
- Handling: Predators handle (e.g. ingesting or digesting) a prey item. Predators remain stationary and do not consume other prey within the area of discovery. Predators shifts from handling into intensive searching mode upon completion of handling time. (Rosenheim and Corbett 2003).
- Attacking: Predator attacks an aphid, and the number of successful attacks is counted. We also counted the total number of contacts with aphids, which allowed calculation of lethal contact (LC) and the search efficiency (SE) index (Table 1).
- Grooming: Predators clean palps on the ground or clean legs with movement of mandibles.

Statistical analyses were performed with MANOVA for overall differences between species and stages (Minorette and Weisser 2000; McPeck 2004). Duration and frequency of intensive and extensive searching, resting, handling and grooming time were all included as dependent variables in the overall multivariate test. Squared-root data were used on dependent variables for statistical analyses to normalize data distribution. If *H. axyridis* was identified as differing significantly from *C. maculata* in the multivariate analysis, the same model was applied to each behavioral variable separately in univariate analyses of variance to determine which variables were responsible for the differences between species (McPeck 2004). The F-approximation of Wilks's λ are presented for the multivariate ANOVA results

(Sokal and Rohlf 1995). Lethal contact (LC) and search efficiency (SE) indices were compared with χ^2 -test.

Table I.1. Formulae of the different developmental and behavioral characteristics measured.

Measures	Unity	Formulae	References
Preimaginal development			
Total survival	%	percentage of larvae emerging as adults	
Adult emergence	%	$\frac{\text{number of adults emerged}}{\text{number of pupae}} \times 100$	Omkar and Srivastava 2003
Growth index (GI)	%/days	$\frac{\% \text{ pupation}}{\text{developmental time}}$	Omkar and Srivastava 2003
Predation efficiency			
Voracity (V)	N aphids/day	number of aphids eaten by day	Lucas et al. 1998
Relative weight gain	mg	$\frac{\text{larval weight}_T (\text{mg}) - \text{larval weight}_{T-1} (\text{mg})}{\text{larval weight}_T (\text{mg})}$	
Relative growth rate (RGR)	mg/days	$\frac{\text{initial adult weight (mg)} - \text{initial L4 weight (mg)}}{\text{developmental time}}$	Omkar and Srivastava 2003
Conversion efficiency (CE)	%	$\frac{\text{weight of predator during development (mg)}}{\text{weight of ingested biomass (mg)}}$	Schanderl 1987
Lethal contact (LC)	%	$\frac{\text{number of contacts resulting in the death of aphids}}{\text{total number of aphids contacted}}$	Lucas et al. 1997
Search efficiency (SE)	%	$\frac{\text{total number of aphids contacted}}{\text{total number of aphids on the plant}}$	
T : time at end of larval stage; $T-1$: time at beginning of larval stage			

I.4 RESULTS

Preimaginal development

No differences between *H. axyridis* and *C. maculata* were observed for total survival (*H. axyridis*: 80.0%; *C. maculata*: 86.7%; $\chi^2 = 1.05$, df = 1, P = 0.31), adult emergence from pupae (*H. axyridis*: 92.3%; *C. maculata*: 100%; $\chi^2 = 1$, df = 1, P = 0.32) and growth index (*H. axyridis*: 4.54%/days; *C. maculata*: 4.28%/days; $\chi^2 = 1$, df = 1, P = 0.32).

Developmental time of *H. axyridis* was shorter than *C. maculata* for the eggs ($F_{1,24} = 21.30$, P < 0.0001), for the 2nd larval instar ($F_{1,23} = 13.22$, P = 0.001) and for the 3rd larval instar ($F_{1,23} = 4.49$, P = 0.045) (Figure 1). The developmental time from eggs to 4th larval instar was also shorter for *H. axyridis* than *C. maculata* ($F_{1,23} = 14.09$, P = 0.001) (Figure 1). The pupation time was longer for *H. axyridis* than *C. maculata* ($F_{1,23} = 25.50$, P < 0.001) (Figure 1). The total preimaginal developmental time of egg to adult of *H. axyridis* was however not significantly different from *C. maculata* ($F_{1,23} = 3.55$, P = 0.070) (Figure 1).

Predation efficiency

Harmonia axyridis consumed more number of aphids compared to *C. maculata* during the 2nd larval instar ($F_{1,62} = 10.87$, P = 0.002), the 3rd ($F_{1,58} = 40.90$, P < 0.0001) and the 4th ($F_{1,83} = 44.46$, P < 0.0001) (Figure 2a). *Harmonia axyridis* consumed 50% more aphids (185 ± 11.5) than *C. maculata* (91.92 ± 5.06) during the complete development ($F_{1,203} = 7.87$; P = 0.006). Relative weight gain of *H. axyridis* was higher in 2nd instar compared to *C. maculata* ($F_{1,62} = 12.60$; P = 0.001) (Figure 2b). Relative growth rate (RGR) of *H. axyridis* ($0.79 \text{ mg/day} \pm 0.11$) during the total development was significantly higher than that of *C. maculata* ($0.25 \text{ mg/day} \pm 0.03$) ($F_{1,24} = 23.46$, P < 0.0001). There was higher conversion efficiency during the 2nd larval instar of *H. axyridis* compared to *C. maculata* ($F_{1,62} = 4.44$; P = 0.039) (Figure 2c).

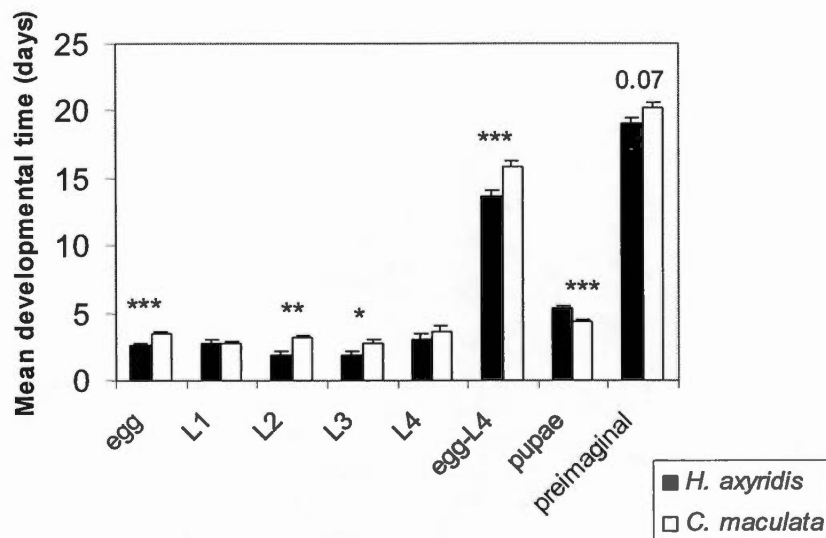


Figure I.1. Developmental time (days \pm SE) by instars of *H. axyridis* and *C. maculata* on *A. pisum* on broadbean plants. Note: * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

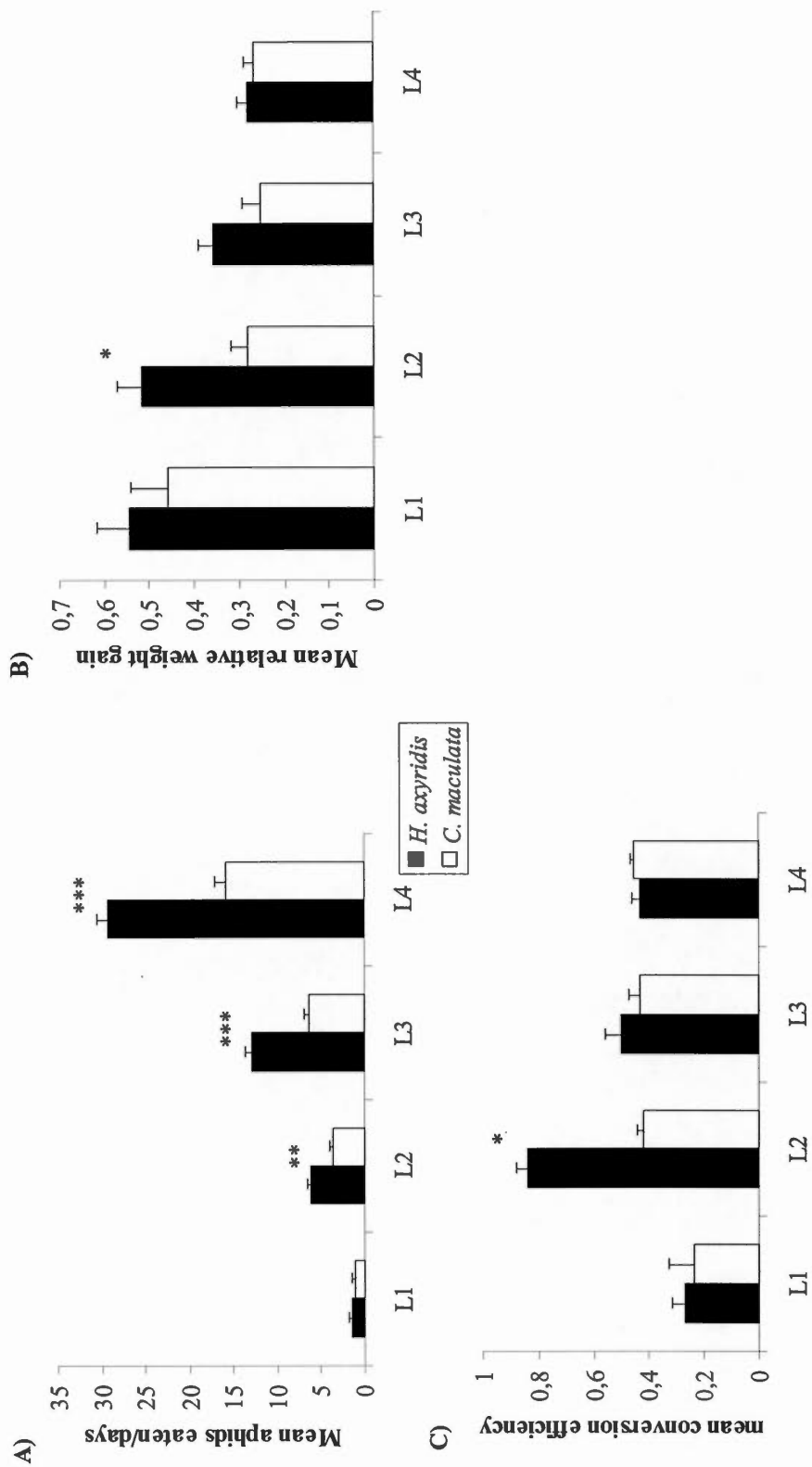


Figure I.2. Predation efficiency of each instars of *H. axyridis* and *C. maculata* on *A. pisum* on broadbean plants. (a) Voracity (N aphids/days \pm SE). (b) Relative weight gain (mg \pm SE). (c) Conversion efficiency (Larval weight (g)/ingested biomass (g) \pm SE). Note: * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Foraging behavior

Duration of behaviors was significantly different between species and developmental stages (Table 2a). While there were no species differences in the duration of foraging behaviors of 1st, 2nd and 3rd larval instars, there were higher handling (ANOVA, $F_{1,22} = 5.06$, $P = 0.035$) and grooming times (ANOVA, $F_{1,22} = 5.83$, $P = 0.025$) for *H. axyridis* than *C. maculata* in the 4th larval instar (Figure 3a). *Coleomegilla maculata* had longer extensive searching time ($F_{1,22} = 17.13$, $P = 0.001$) as 4th larval instar than *H. axyridis* (Figure 3a).

The whole model of MANOVA was significantly different for the occurrence of behavioral variables between species and stages (Table 2b). There was also a significant interaction between species and stages for the occurrence of behaviors (Table 2b). There were no differences in the occurrence of foraging behaviors of the 1st, 2nd and 3rd larval instars of the two coccinellid species. There was however higher handling occurrence ($F_{1,22} = 10.78$, $P = 0.004$) and higher attacking occurrence ($F_{1,22} = 6.99$, $P = 0.015$) for *H. axyridis* than *C. maculata* in the 4th larval instar (Figure 3b). There was also higher resting occurrence ($F_{1,22} = 10.39$, $P = 0.004$) and higher extensive searching occurrence ($F_{1,22} = 14.11$, $P = 0.001$) for *C. maculata* in this larval instar (Figure 3b).

The lethal contact index was not different between the two species for 1st ($\chi^2 = 0.39$, $df = 1$, $P = 0.53$), 2nd ($\chi^2 = 0.59$, $df = 1$, $P = 0.44$) and 3rd ($\chi^2 = 0.13$, $df = 1$, $P = 0.72$) larval instars. Following an attack, *H. axyridis* was more efficient at killing its prey than *C. maculata* in the 4th larval instar ($\chi^2 = 6.77$, $df = 1$, $P = 0.009$) (Figure 3c). The search efficiency index was not different between the two species for 1st ($\chi^2 = 0.17$, $df = 1$, $P = 0.68$), 2nd ($\chi^2 = 0.14$, $df = 1$, $P = 0.71$) and 3rd ($\chi^2 = 0.99$, $df = 1$, $P = 0.32$) larval instars. *Harmonia axyridis* was however more efficient in finding its prey than *C. maculata* in the 4th larval instar ($\chi^2 = 7.38$, $df = 1$, $P = 0.007$) (Figure 3d).

Fifth larval instar

Four individuals (33%) of *H. axyridis* molted to 5th larval instars, but no difference in total developmental time of these individuals was observed compared to the other 8 (Wilcoxon test: $z = -0.97$, $P = 0.33$) (Figure 4a). Moreover, preimaginal time development from egg to the last instar (fourth or fifth) was not different between the two groups (Wilcoxon test: $z = -1.67$, $P = 0.095$) (Figure 4a). All individuals of the 5th larval instar were females which exhibited increased voracity (Wilcoxon test: $z = 3.26$, $P = 0.0011$), a greater body mass (Wilcoxon test: $z = 2.54$, $P = 0.011$) (Figure 4b), and an increased weight gain (Wilcoxon test: $z = 3.05$, $P = 0.002$) (Figure 4b) than individuals that completed only a 4th larval instar. Relative weight gain and conversion efficiency were not different between 4th and 5th instar of *H. axyridis*. Duration and frequency of foraging behaviors of 5th instar larvae were not different from the 4th instars. Lethal contact and search efficiency indices of 5th instar larvae were not different from the 4th instar. *Harmonia axyridis* larvae that achieved a 5th larval instar were heavier as adults than larvae that completed a 4th larval instar (Wilcoxon test: $z = 3.67$, $P = 0.0002$) (Figure 4b).

Table I.2. Statistical results for MANOVA on time (A) and occurrence (B) of foraging behavior between *H. axyridis* and *C. maculata*.

A	Value	Approx. F	NumDF	DenDF	Prob>F
Whole model					
Wilks' Lambda	0.2257	5.353	36	395.22	< 0.0001
Species					
F Test	0.1668	4.3777	4	105	0.0026
Stages					
Wilks' Lambda	0.2917	9.9782	16	321.42	< 0.0001
Species x Stages					
Wilks' Lambda	0.8092	1.4413	16	321.42	0.1206
B					
Whole model					
Wilks' Lambda	0.2205	5.4564	36	395.22	< 0.0001
Species					
F Test	0.4125	10.828	4	105	< 0.0001
Stages					
Wilks' Lambda	0.3763	7.5748	16	321.42	< 0.0001
Species x Stages					
Wilks' Lambda	0.6562	2.9699	16	321.42	0.0001

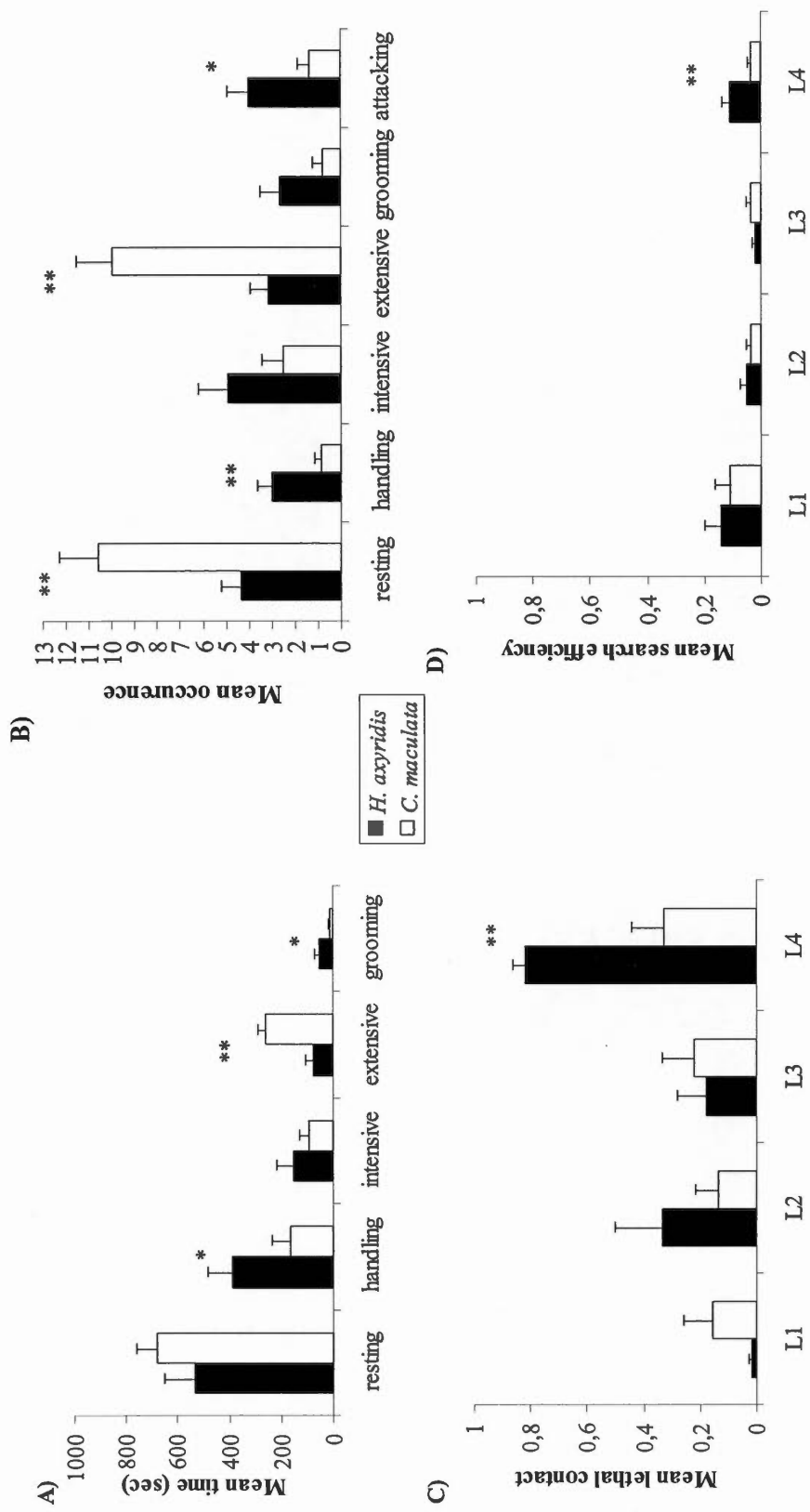


Figure I.3. Foraging behaviors of *H. axyridis* and *C. maculata* on broadbean plants after each molt. (a) Mean time (sec \pm SE) of behaviors of 4th instar larvae. (b) Occurrence of behaviors (mean \pm SE) of 4th instar larvae. (c) Mean lethal contact (number of contact resulting in death of aphids/total contact number) of 4th instar larvae. (d) Mean search efficiency (number of aphids contacted/ total number of aphids on plants) of 4th instar larvae. Note: * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

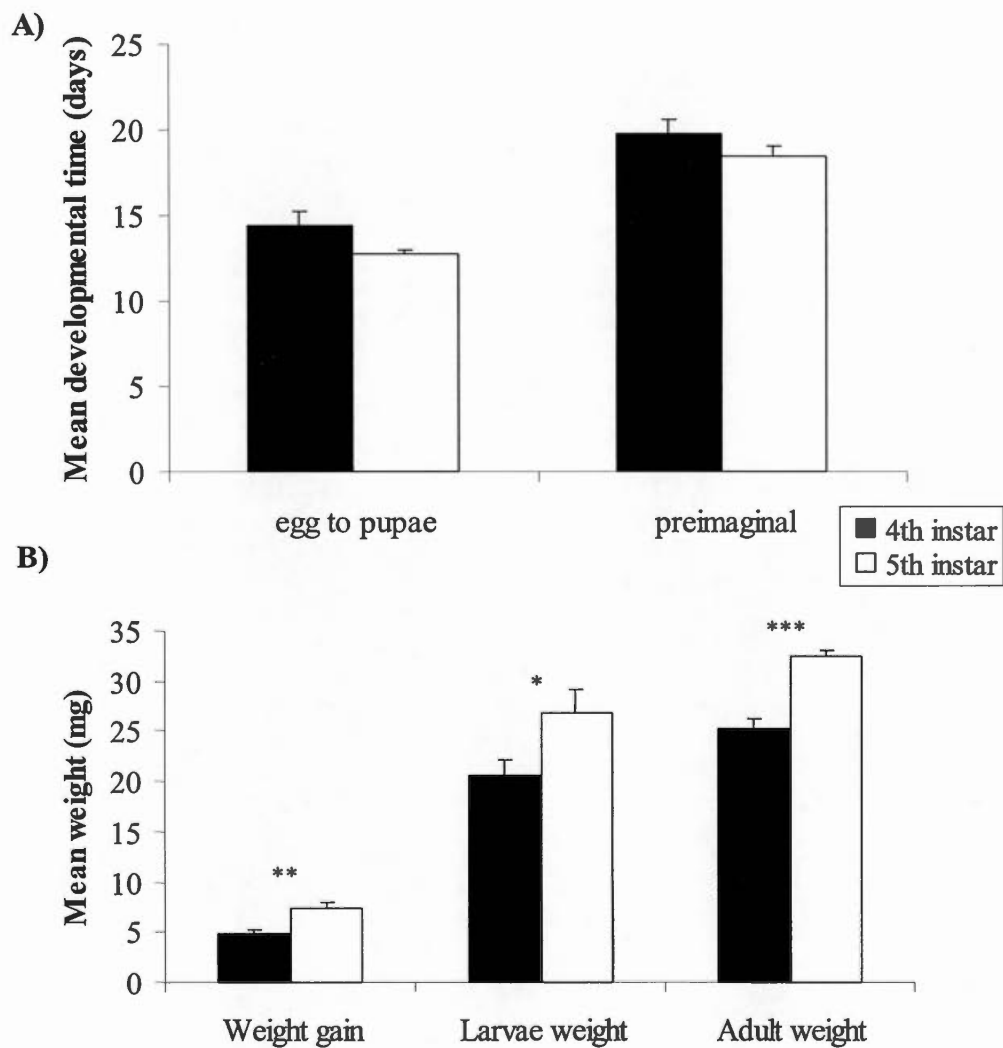


Figure I.4. Developmental characteristics of the 5th instars of *H. axyridis* compared to the 4th. (a) Developmental time (days \pm SE). (b) Mean weight gain, larvae and adult weight (mg \pm SE). Note: * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

I.5 DISCUSSION

Both developmental and behavioral characteristics of *H. axyridis* were different from the indigenous *C. maculata* and may explain the invasiveness of the multicolored Asian lady beetle. We demonstrated a shorter development during the 2nd larval instar, a faster development to the 4th larval instar, and the occurrence of a 5th larval instar for *H. axyridis*. The predation efficiency of *H. axyridis* was higher than *C. maculata*. *Harmonia axyridis* 4th larval instar searched and attacked prey more efficiently than *C. maculata*.

Despite no significant difference in the total preimaginal developmental time (but $P = 0.07$), several interesting differences between the two coccinellid species were observed. *Harmonia axyridis* developed more rapidly during the 2nd larval instar and reached the 4th instar faster than *C. maculata*. Young coccinellid larvae of 1st and 2nd instar cannot actively defend themselves against predation (Hodek and Honěk 1996; Lucas *et al.* 1997b; 1998; Lucas 2005). Cannibalism and intraguild predation cause significant mortality at these young instars, particularly for *H. axyridis*, which experience a relatively high incidence of cannibalism (Burgio *et al.* 2002; Michaud 2003). A faster development to 3rd and 4th instar should increase survival chances and consequently give an advantage for the individuals that came rapidly through this vulnerable stage. *Harmonia axyridis* attained also more rapidly the 4th instar, which is characterized by strong predation activities (Yasuda and Ohnuma 1999; Yasuda *et al.* 2001; Lanzoni *et al.* 2004). This factor, coupled with the reduction of vulnerability of 2nd instars may constitute an advantage for the exotic species. This experiment did not show, however, a more rapid preimaginal developmental time for *H. axyridis* compared to the indigenous species. This result appears also in the experiment of Lanzoni *et al.* (2004) in Italy when they compared *H. axyridis* with the indigenous species *Hippodamia variegata* (Goeze) and *Adalia bipunctata* (L.). Pupation time of *H. axyridis* was longer than *C. maculata* and can explain lack of difference in the preimaginal developmental time. The pupation is another vulnerable stage during

development in ladybeetles, but with lower vulnerability than first instars because they pupate in retired places, with lesser chances to be found and consumed or parasitized and with their ability to flick up and down (Majerus 1994; Lucas *et al.* 2000). Simultaneously obtaining enough food to grow and reproduce while avoiding predation is a pervasive trade-off faced by many organisms (McPeck 2004). *Harmonia axyridis* seems to perform this trade-off with its developmental pattern and this could explain its invasive success.

Confirming our second hypothesis, *H. axyridis* presented greater predation efficiency than *C. maculata*. *Harmonia axyridis* consumed significantly more pea aphids than *C. maculata* during almost all instars. Furthermore, relative growth rate during preimaginal development was higher for *H. axyridis*, indicating that the invasive species can accumulate higher biomass in a shorter period of time than the native species. This may facilitate exploitation of pests with rapid population fluctuations such as aphid outbreak (Schellhorn and Andow 1999). Weight gained by each species is determined by its physiological ability to convert assimilated food into its own biomass (Dixon and Hemptinne 2001). Large ladybird beetles need less biomass of aphids per unit area for satiation than do small ladybird beetles because of higher searching efficiency (Dixon and Stewart 1991). It follows that larger ladybird beetles will have higher conversion efficiency and thus require a lower amount of aphid biomass to develop (Dixon and Stewart 1991; Kozłowski and Weiner 1997). Conversion efficiency of *H. axyridis* was higher than *C. maculata* in 2nd larval instar. Higher conversion efficiency in 2nd instar can explain the faster developmental time and would give a strong advantage to the invasive species to avoid predation during this vulnerable stage. Higher resource conversion efficiency can also increase exploitative competition ability and increase population density of the invading species (Byers 2000). *H. axyridis* benefits from both these mechanisms.

Behavioral observations of coccinellid larvae confirmed higher predatory efficiency of *H. axyridis* as 4th instar than *C. maculata*. It is thought that a more

efficient predator attacks a larger proportion of prey population over a given period of time (Dixon 2000). Lethal contact proportion of *H. axyridis* as 4th instar on pea aphids is more than two-times superior ($81.5 \pm 4.7\%$) than *C. maculata* ($32.7 \pm 11.2\%$), indicating that when an aphid is detected, it is almost always killed and eaten by the multicolored Asian lady beetle. *Harmonia axyridis* adults have a high ability to track aphid populations in space and time (Osawa 2000; With *et al.* 2002). Search efficiency of *H. axyridis* as 4th instar on pea aphids ($11.1 \pm 2.2\%$) was more than three-times superior than *C. maculata* (3.5 ± 1.1). Fourth larval instars of *H. axyridis* are also characterized by a lower frequency and duration of extensive searching, but with an increased number of attacks on aphids, an increased lethal contact proportion and searching efficiency on aphids than *C. maculata*. These factors confirmed that *H. axyridis* is a more efficient predator than *C. maculata* in the 4th larval instar.

Fifth larval instars may also promote invasion of *H. axyridis*. Only three coccinellid species were mentioned in the literature having performed 5th larval instars, *C. maculata*, *Chilocorus bipustulatus* L. and *Callicaria superba* Mulsant (Warren and Tadic 1967; Majerus 1994; Hodek and Honěk 1996). Normally, when a 5th larval instar is found in coccinellids, the supposition is that the juveniles have experienced relatively low quality of food and they present a decreased growth rate or adult size (Warren and Tadic 1967; Hodek and Honěk 1996). In our case, individuals with a 5th larval stage developed at the same rate, consumed more aphids and weighted more than other conspecific larvae. Furthermore, adults with 5 instars were heavier than those with 4. Weight of adult coccinellids is positively correlated with reproductive capacity (Stewart *et al.* 1991; Dixon 2000). Therefore, we can suppose that higher weight of 5th larval instar can generate higher reproductive capacity to *H. axyridis*. Occurrence of a 5th larval instar that performed better in the new environment gave a strong advantage for an invasive species that should achieve a higher fecundity and higher population. The occurrence of this 5th larval instar can be a genetic or a phenotypic change following the introduction. Some studies have

shown that species may attain dominance in introduced ranges because they experience rapid genetic changes linked to new selection pressures in the novel environment (Blossey and Nötzold 1995; Sakai *et al.* 2001; Lee 2002; Hänfling and Kollman 2002; Stockwell *et al.* 2003; Hierro *et al.* 2005). The evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold 1995) argues that exotics liberated from their specialist enemies should lose costly traits that confer resistance to their native specialist enemies. Exotics can reallocate resources from the maintenance of resistance to traits, such as size or fecundity, which might be under greater selection in the introduced range (Hierro *et al.* 2005). Thus, EICA predicts that liberation from natural enemies should result in exotics evolving in ways that enhance their performance in new communities. In the case of *H. axyridis*, the occurrence of a 5th larval instar, that give some advantage in body size and in fecundity, can be such genetic change. It seems that there is no effective parasitism by *Dinocampus coccinellae* Shrank (Firlej *et al.* 2005) in Quebec, a parasitoid of many coccinellid species commonly found in Asia and in North America. This coccinellid species seem almost free from predation pressure in our area. The EICA hypothesis can be considered for the multicolored Asian lady beetle. Other hypothesis could also be envisaged to explain the occurrence of a 5th instar such as the bet-hedging strategy or the phenotypic plasticity (West-Eberhard 1989; Scheiner 1993; Dixon 2000; Soula and Menu 2003). Bet-hedging strategy is an adaptation to environmental stochasticity in which more than one phenotype is maintained by a single genotype (Soula and Menu 2003). By contrast, phenotypic plasticity is the variation in the phenotypic expression of a trait induced by environmental conditions, where different adaptative phenotypes are maintained in the same life stage and the same population but not necessarily simultaneously expressed in the same individuals (West-Eberhard 1989; Scheiner 1993; Dixon 2000). Nonetheless, this first observation of the phenomenon in *H. axyridis* warrants further investigation to understand this variation in our area.

The key factors in invasion process are growth of juveniles into the adult stage and survival of adults (Marco *et al.* 2002). Presence of juveniles in high density could accelerate rate of invasion, and is often accompanied by displacement of native species (Marco *et al.* 2002). Our study pointed more precisely which developmental characteristics of the multicolored Asian lady beetle can ensure safer growth of juveniles and higher density of adults in the environment. Studies of juvenile characteristics before introduction of biological control agents or after arrival of a new species can improve our knowledge of the invasion process and prediction of successful invaders. Some characteristics such as better searching abilities and faster developmental time in introduced biological control agents had shown positive correlation with non target effects (Kimberling 2004). We demonstrated that all these characteristics were present in the multicolored Asian lady beetle. Some negative impacts on native fauna had been shown after its arrival in North America (Tedders and Schaefer 1994; Brown and Miller 1998; Colunga-Garcia and Gage 1998; Michaud 2002; Reitz and Trumble 2002; Snyder *et al.* 2004). We can expect nontarget effects of the arrival and spread of this species in our country. Survival of adults is also important in invasion process (Marco *et al.* 2002). Our study had shown that some larvae presented higher weight in adults and possibility of higher fecundity with the occurrence of a supernumerary larval instar that may ensure higher population growth and density. Survival of juveniles and adults is greatly influenced by habitat invasibility, e.g. different resource availability for the species as food, habitat suitability or quality of overwintering sites (Hierro *et al.* 2005; Marco *et al.* 2002). Survival of this species related to competitive ability, winter survival and resources exploitation are currently under study and will make an entire portrait of this invasive species, with better understanding of invasion process.

I.6 ACKNOWLEDGEMENTS

This research was supported by an NSERC scholarship granted to G. Labrie, NSERC grant to D. Coderre and E. Lucas. We thank Annie-Ève Gagnon and Raphaël Dubé for their technical assistance. We also thank the Laboratoire de lutte biologique of UQAM for revision of the manuscript and Tim Work for revision of the manuscript.

I.7 REFERENCES

- Alyokhin, A. and Sewell, G. (2004) Changes in a lady beetle community following the establishment of three alien species. *Biological Invasions* **6**, 436-471.
- Blossey, B. and Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-889.
- Brown, M.W. and Miller, S.S. (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News*, **109**, 143-151.
- Brown, M.W. (2003) Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl*, **48**, 141-153.
- Burgio, G., Santi, F. and Maini, S. (2002) On intraguild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). *Biological Control*, **24**, 110-116.
- Byers, J.E. (2000) Competition between two estuarine snails: implications for invasions of exotic species. *Ecology*, **81**, 1225-1239.
- Chapin, J.B. and Brou, V.A. (1991) *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, **93**, 630-635.
- Coderre, D., Lucas, E. and Gagne, I. (1995) The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) in Canada. *The Canadian Entomologist*, **127**, 609-611.
- Colunga-Garcia, M. and Gage, S.H. (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology*, **27**, 1574-1580.
- Cottrell, T.E. and Yeargan, K.V. (1998) Intraguild predation between an introduced lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Journal of the Kansas Entomological Society*, **71**, 159-163.

- Cottrell, T.E. and Shapiro-Ilan, D.I. (2003) Susceptibility of a native and an exotic lady beetle (Coleoptera: Coccinellidae) to *Beauveria bassiana*. *Journal of Invertebrate Pathology*, **84**, 137-144.
- Cottrell, T.E. (2004) Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biological Control*, **31**, 362-371.
- Dixon, A.F.G. (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia bipunctata* (L.) *Journal of Animal Ecology*, **28**, 259-281.
- Dixon, A.F.G. (2000) Insect predator-prey dynamics: ladybird beetles and biological control. Cambridge University Press, Cambridge.
- Dixon, A.F.G. and Hemptinne, J.L. (2001) Body size distribution in predatory ladybird beetles reflects that of their prey. *Ecology*, **82**, 1847-1856.
- Dixon, A.F.G. and Stewart, L.A. (1991) Size and foraging in ladybird beetles. In Polgar, L., Chambers, R.J., Dixon, A.F.G. and Hodek, I. (Eds) Behaviour and impacts of Aphidophaga. SPB Academic Publishing bv, The Hague, The Netherlands. p. 123-132.
- Ettifouri, M. and Ferran, A. (1993) Influence of larval rearing diet on the intensive searching behaviour of *Harmonia axyridis* (Col: Coccinellidae) larvae. *Entomophaga*, **38**, 51-59.
- Félix, S. and Soares, A.O. (2004) Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of body weight. *European Journal of Entomology*, **101**, 237-242.
- Firlej, A., Boivin, G., Lucas, E. and Coderre, D. (2005) First report of *Harmonia axyridis* being attacked by *Dinocampus coccinellae* Schrank in Canada. *Biological Invasion*,
- Gordon, R.D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of New York Entomological Society*, **93**, 1-912.

- Hänfling, B. and Kollmann, J. (2002) An evolutionary perspective of biological invasion. *Trends in Ecology and Evolution*, **17**, 545-546.
- Hierro, J.L., Maron, J.L., Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced *and* native range. *Journal of Ecology*, **93**, 5-15.
- Hodek, I. and Honěk, A. (1996) Ecology of Coccinellidae. Kluwer Academic Publishers, Netherlands.
- Hoogendoorn, M. and Heimpel, G.E. (2002) Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. *Biological Control*, **25**, 224-230.
- Hoogendoorn, M. and Heimpel, G.E. (2004) Competitive interactions between an exotic and a native ladybeetle: a field cage study. *Entomologia Experimentalis et Applicata*, **111**, 19-28.
- Iablokoff-Khnzorian, S.M. (1982) Les coccinelles, Coléoptères-Coccinellidae. Société Nouvelle des Éditions Boubée, Paris.
- Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164-170.
- Kimberling, D.N. (2004) Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. *Biological Invasion*, **6**, 310-318.
- Koch, R.L. (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science*, **3**, 1-16.
- Kolar, C.S. and Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199-204.
- Kozłowski, J. and Wiener, J. (1997) Interspecific allometries are by-products of body size optimization. *The American Naturalist*, **149**, 352-380.
- Krijger, C.L., Peters, Y.C. and Sevenster, J.G. (2001) Competitive ability of neotropical *Drosophila* predicted from larval development times. *Oikos*, **92**, 325-

332.

- Lanzoni, A., Accinelli, G., Bazzocchi, G.G. and Burgio, G. (2004) Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Col. Coccinellidae). *Journal of Applied Entomology*, **128**, 298-306.
- Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends in Ecology and Evolution*, **17**, 386-391.
- Lucas, E., Coderre, D. and Vincent, C. (1997a) Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. *Entomologia Experimentalis et Applicata*, **85**, 151-159.
- Lucas, E., Coderre, D. and Brodeur, J. (1997b) Instar-specific defense of *Coleomegilla maculata lengi* (Col. : Coccinellidae) : influence on attack success of the intraguild predator *Chrysoperla rufilabris* (Neur. : Chrysopidae). *Entomophaga*, **42**, 3-12.
- Lucas, E., Lapalme, S. and Coderre, D. (1998) Voracité comparative de trois coccinelles prédatrices contre le tétranyque rouge du pommier (Acarina: Tetranychidae). *Phytoprotection*, **78**, 117-123.
- Lucas, E., Coderre, D. and Brodeur, J. (2000) Selection of molting and pupation sites by *Coleomegilla maculata* (Coleoptera: Coccinellidae): avoidance of intraguild predation. *Environmental Entomology*, **29**, 454-459.
- Lucas, E., Gagné, I. and Coderre, D. (2002) Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **99**, 457-463.
- Lucas, E. (2005) Intraguild predation among aphidophagous predators. *European Journal of Entomology*, **102**, 351-364.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. and Bazzaz, F.A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689-710.
- Majerus, M.E.N. (1994) Ladybirds. Harper Collins Publishers, Toronto.

- Marco, D.E., Paez, S.A. and Cannas, S.A. (2002) Species invasiveness in biological invasions: a modelling approach. *Biological Invasion*, **4**, 193-205.
- McPeck, M.A. (2004) The growth/predation risk trade-off: so what is the mechanism? *American Naturalist*, **163**, E88-E111.
- Michaud, J.P. (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. *Environmental Entomology*, **31**, 827-835.
- Michaud, J.P. (2003) A comparative study of larval cannibalism in three species of ladybird. *Ecological Entomology*, **28**, 92-101.
- Minoretti, N. and Weisser, W.W. (2000) The impact of individual ladybirds (*Coccinella septempunctata*, Coleoptera : Coccinellidae) cell aphid colonies. *European Journal of Entomology*, **97**, 475-479.
- Munyanza, J. and Obrycki, J.J. (1998a) Development of three populations of *Coleomegilla maculata* (Coleoptera, Coccinellidae) feeding on eggs of Colorado Potato Beetle (Coleoptera, Chrysomelidae). *Environmental Entomology*, **27**, 117-122.
- Munyanza, J. and Obrycki, J.J. (1998b) Searching behavior of *Coleomegilla maculata* larvae feeding on Colorado Potato Beetle eggs. *Biological Control*, **13**, 85-90.
- Musser, F.R. and Shelton, A.M. (2003) Factors altering the temporal and within-plant distribution of coccinellids in corn and their impact on potential intraguild predation. *Environmental Entomology*, **32**,: 575-583.
- Noldus Information Technology b.v. 1989, 1990. The Observer 2.0. University Business and Technology Center, The Netherlands.
- Omkar, and Srivastava, S. (2003) Influence of six aphid prey species on development and reproduction of a ladybird beetle, *Coccinella septempunctata*. *BioControl*, **48**, 379-393.

- Osawa, N. (2000) Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera : Coccinellidae): resource tracking and population characteristics. *Population Ecology*, **42**, 115-127.
- Pimentel, D., Lach, L., Zuniga, R. and Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience*, **50**, 53-65.
- Reitz, S.R. and Trumble, J.T. (2002) Competitive displacement among insects and arachnids. *Annual Review of Entomology*, **47**, 435-465.
- Rosenheim, J.A. and Corbett, A. (2003) Omnivory and the indeterminacy of predator function: can a knowledge of foraging behavior help? *Ecology*, **84**, 2538-2548.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305-332.
- Schanderl, L.H., Ferran, A., Larroque, M.M. (1985) Les besoins trophiques et thermiques des larves de la coccinelle *Harmonia axyridis* Pallas. *Agronomie*, **5**, 417-422.
- Scheiner, S.M. (1993) Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, **24**, 35-68.
- Schellhorn, N.A. and Andow, D.A. (1999) Mortality of coccinellid (Coleoptera : Coccinellidae) larvae and pupae when prey become scarce. *Environmental Entomology*, **28**, 1092-1100.
- Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170-176.
- Snyder, W.E., Clevenger, G.M. and Eigenbrode, S.D. (2004) Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia*, **140**, 559-565.
- Soares, A.O., Coderre, D. and Schanderl, H. (2001) Fitness of two phenotypes of *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **98**, 287-293.

- Sokal, R.R. and Rohlf, F.J. (1995) Biometry: the principles and practice of statistics in biological research. 3rd Edition. W. H. Freeman, San Francisco.
- Soula, B. and Menu, F. (2003) Variability in diapause duration in the chestnut weevil : mixed ESS, genetic polymorphism or bet-hedging? *Oikos*, **100**, 574-580.
- Stewart, L.A., Hemptinne, J.-L. and Dixon, A.F.G. (1991) Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Functional Ecology*, **5**, 380-385.
- Stockwell, C.A., Hendry, A.P. and Kinnison, M.T. (2003) Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*, **18**, 94-101.
- Tedders, W.L. and Schaefer, P.W. (1994) Release and establishment of *Harmonia axyridis* (Coleoptera, Coccinellidae) in the Southeastern United-States. *Entomological News*, **105**, 228-243.
- Turnock, W.J., Wise, I.L. and Matheson, F.O. (2003) Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. *The Canadian Entomologist*, **135**, 391-404.
- Vitousek, P.M., Dantonio, C.M., Loope, L.L. and Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist*, **84**, 468-478.
- Warren, L.O. and Tadic, M. (1967) Biological observations on *Coleomegilla maculata* and its role as a predator of the fall webworm. *Journal of Economic Entomology*, **60**, 1492-1496.
- West-Eberhard, M.J. (1989) Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, **20**, 249-278.
- With, K., Pavuk, D.M., Worchuck, J.L., Oates, R.K. and Fisher, J.L. (2002) Threshold effect of landscape structure on biological control in agroecosystems. *Ecological Applications*, **12**, 52-65.
- Yasuda, H. and Ohnuma, N. (1999) Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia Experimentalis et Applicata*, **93**, 63-67.
- Yasuda, H., Kikuchi, T., Kindlmann, P. and Sato, S. (2001) Relationships between

attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior*, **14**, 373-384.

CHAPITRE II

**MAY COMPETITIVE ABILITIES OF *HARMONIA AXYRIDIS*
EXPLAIN ITS INVASIVE SUCCESS?**

II.1 ABSTRACT

Intraguild predation (IGP), the killing and eating of a species that use similar resources and are potential competitors, is a common interaction of invasive species on indigenous one. The multicoloured Asian ladybeetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), a species introduced in North America for biological control purposes, have shown in many studies an advantage in IGP over a dozen of species. Our study aimed to evaluate IGP of all instars of *H. axyridis* with two functionally similar ladybeetle in the Montreal, Quebec, area, the indigenous *Coleomegilla maculata lengi* Timberlake and the invasive *Propylea quatuordecimpunctata* L. Indirect sublethal effects on weight were also evaluated when *H. axyridis* and *C. maculata* larvae of similar size were held on plants together and defensive behaviors were also observed. Our first hypothesis was that *H. axyridis* is a more effective intraguild predator than *C. maculata* or *P. quatuordecimpunctata*. Our second hypothesis was that *H. axyridis* presence would lead to increased sublethal effects such as weight loss of *C. maculata*. In our study, intraguild predation (IGP) was mutual for the three combinations, but mainly asymmetrical in favour of *H. axyridis*. IGP was observed in 59% of the combinations between *H. axyridis* and *C. maculata*, *H. axyridis* and *P. quatuordecimpunctata*, and in 58% between *P. quatuordecimpunctata* and *C. maculata*. *Harmonia axyridis* 4th instar larvae and pupae were never preyed upon, neither by *C. maculata* nor by *P. quatuordecimpunctata*, while *H. axyridis* preyed on all instars of these two species. *Harmonia axyridis* eggs and younger larvae were however susceptible to predation. Egg predation experiments demonstrated that predator species were not reluctant to consume other species' eggs and that almost 100% of the eggs were consumed by older instars and adults. IGP intensity increased with weight differences in the two combinations with *H. axyridis*, but not between *P. quatuordecimpunctata* and *C. maculata*. No IGP were observed on plants with similar-sized larvae of *H. axyridis* and *C. maculata*. Likewise no indirect sublethal effect on weight were observed.

Defensive mechanisms were similar for the two species, dropping-off the plant or running after an attack. These results suggest that *H. axyridis* is a more effective intraguild predator than *C. maculata* or *P. quatuordecimpunctata*, but could be vulnerable to intraguild predation in younger instars. However, its aggressiveness and the low vulnerability of later instars and pupae to predation may contribute to its great ability to invade new habitats.

Key words: *Harmonia axyridis*, intraguild predation, top-predator, invasive species, *Coleomegilla maculata lengi*, *Propylea quatuordecimpunctata*, indirect sublethal effects

II.2 INTRODUCTION

Invasive species are now recognized to cause major economic, biological and irrevocable impacts throughout the world (Lodge *et al.* 2006; Simberloff 2005). Costs of these invasive species range between \$314 billion in USA and \$7.5 billion in Canada each year (Colautti *et al.* 2006; Dawson 2002; Pimentel *et al.* 2000, 2001). Biological impact include direct and indirect competition with native species, and further displacement or extinction (Reitz and Trumble 2002; Sakai *et al.* 2001; Shea and Chesson 2002). Although recent emphasis on experimental studies is yielding important insights on competitive effects of invasive species (Bando 2006; Hoogendoorn and Heimpel 2004; Kiesecker *et al.* 2001), the ecological mechanisms for such displacements have generally been difficult to define (Evans 2004; Mack *et al.* 2000). Competitive interactions with native species influence the establishment and spread of invasive populations (e.g., Corbin and D'Antonio 2004). It is hypothesized that, unless resources are spatially or temporally partitioned, species with similar resource and habitat requirements are predicted to compete intensively (Bando 2006; Dudgeon *et al.* 1999). Thus, strong competition is expected to arise between functionally similar native and invasive species (Bando 2006).

Intraguild predation (IGP) is the killing and eating of species that use similar resources and are potential competitors (Polis *et al.* 1989). This interaction is very common and important in an array of communities (Arim and Marquet 2004; Holt and Polis 1997; Polis *et al.* 1989). In a guild, an intraguild predator preys on a competitor, the intraguild prey, and each species prey on a common resource, the extraguild prey. It is now well established that IGP affect the intraguild predator, the intraguild prey and the extraguild prey at the individual, the population and the community levels (Lucas 2005). Many factors will influence IGP intensity and direction. Environmental characteristics, such as spatial scales of investigation (Petri dishes versus plants), presence of refuges or human activity (use of pesticides), could reduce or enhance intensity of interaction (e.g. Fr  chette *et al.* 2007; Hindayana *et al.*

2001; Lucas 2005; Provost *et al.* 2003). Plants may provide refuges for the intraguild prey or may reduce predator mobility, reducing intraguild predation intensity (Lucas and Brodeur 1999). Mobility of the intraguild prey (Lucas *et al.* 1998), efficient escape behavior (Yasuda *et al.* 2001) or choice of secure pupating places (Félix and Soares 2004; Lucas *et al.* 1998; 2000) can reduce IGP. The relative size of intraguild predator and prey will often determine the outcome of the interaction, with larger individuals preying on smaller ones (Félix and Soares 2004; Lucas *et al.* 1998; Sato *et al.* 2005). Even in absence of IGP, sublethal indirect effects could be observed (Lucas 2005), such as slowed developmental time (Lucas and Alomar 2002a, b; Yasuda and Kimura 2001) or decreased foraging activity (Okuyama 2002). Sublethal effects are however rarely considered in IGP studies (Lucas 2005).

Invasive species can generate new interactions with indigenous species and IGP is likely to occur. A current case is that of the multicoloured Asian ladybeetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), introduced in the United States of America in 1916 (Gordon 1985) and now invading North America (Alyokhin and Sewell 2004; Coderre *et al.* 1995; Colunga-Garcia and Gage 1998; LaMana and Miller 1996; Tedders and Schaefer 1994; Turnock *et al.* 2003) and many other countries throughout the world (Adriaens *et al.* 2003; de Almeida and da Silva 2002; Majerus *et al.* 2006; Saini 2004; San Martin *et al.* 2005). *Harmonia axyridis* have shown in many studies an advantage in both interference competition and predation over a dozen of species (Koch 2003; Lucas 2005; Lucas *et al.* Annexe B; Pervez and Omkar 2006). Experiments in laboratory have shown that *H. axyridis* was an important intraguild predator that could negatively impact native or other invasive species. For example, the ladybeetle *Adalia bipunctata* L. was heavily preyed upon by *H. axyridis* in laboratory (Burgio *et al.* 2002; Kajita *et al.* 2000; Sato and Dixon 2004). Other native species, such as *Coccinella undecimpunctata* L. (Félix and Soares 2004), *Olla v-nigrum* Mulsant (Michaud and Grant 2003), *Cycloneda sanguinea* L. (Michaud 2002), *Propylea japonica* L. (Yasuda and Kimura 2001), or *Coleomegilla*

maculata DeGeer (Cottrell and Yeargan 1998, Cottrell 2004; Hoogendoorn and Heimpel 2004) were also affected in laboratory or in the field by *H. axyridis*. *Coccinella septempunctata* L., another invasive species in North America that cause serious threat to native species (Elliott *et al.* 1996; Ellis *et al.* 1999; Evans 2004; Wheeler and Hoebeke 1995), was negatively affected through intraguild predation by *H. axyridis* (Hironori and Katsuhiko 1997; Kajita *et al.* 2000; Phoofolo and Obrycki 1998; Yasuda and Kimura 2001; Yasuda and Ohnuma 1999; Yasuda *et al.* 2001). This species was assigned the rank of top predator as eggs and larvae of this species should be well defended against intraguild predators (Dixon 2000). Negative impacts on native coccinellid species by *H. axyridis* are thus expected relative to its competitive abilities (Brown and Miller 1998; Hoogendoorn and Heimpel 2004).

North American species which are functionally similar to *H. axyridis* could thus be threaten by this invasive species. The indigenous *C. maculata* was observed in the field in similar spatial and temporal niches than *H. axyridis* (Hoogendoorn and Heimpel 2004; Labrie *et al.* unpublished data; Musser and Shelton 2003; Nault and Kennedy 2003; Park and Obrycki 2004). Several laboratory experiments demonstrated that *H. axyridis* preyed on *C. maculata* eggs (Cottrell 2004; Cottrell and Yeargan 1998) and larvae (Cottrell and Yeargan 1998) but no experiments have tested IGP over all instars of the two species. It is however dangerous to assess the status and impacts of a species without testing all stages. Another exotic species, *Propylea quatuordecimpunctata* L. was found in similar spatial and temporal niche of *H. axyridis* in corn, soybean and potato crop in North America (Alyokhin and Sewell 2004; Fox *et al.* 2005; Labrie *et al.* unpublished data; Lucas *et al.* Annexe A; Mignault *et al.* 2006; Musser and Shelton 2003). *Propylea quatuordecimpunctata* was first seen in 1968 near Quebec, Canada and further spread in northeastern United States (Day *et al.* 1994; Gordon 1985). A significant negative relationship was observed between the establishment of *P. quatuordecimpunctata* and *H. axyridis* on the abundance of the indigenous *Coccinella transversoguttata* Brown in Maine, USA

(Alyokhin and Sewell. 2004). Few studies evaluated IGP between invasive species and no studies evaluated IGP between *H. axyridis* and *P. quatuordecimpunctata* or between this invasive species and an indigenous species like *C. maculata*. We measure IGP intensity, direction and symmetry between the invasives *H. axyridis*, *P. quatuordecimpunctata* and the indigenous *C. maculata*. We hypothesized that *H. axyridis* will be a better intraguild predator than the two other ladybeetles. Also, if this species is a top-predator, little or no IGP will be observed on any stages (Dixon 2000). Sublethal indirect effects of IGP between *H. axyridis* and *C. maculata* were also measured in an experiment on young corn plant. Our second hypothesis stated that the presence of *H. axyridis* will lead to weight loss of *C. maculata* by indirect effect of IGP.

II.3 MATERIAL AND METHODS

Experiments were carried out between 2001 and 2003 to evaluate IGP between *H. axyridis*, *C. maculata* and *P. quatuordecimpunctata*.

Adults of P14 were collected at the border of a cruciferous field in Sherington region of Quebec (45° 09' 59" 73° 31' 32") in 2001. HA and CM individuals were collected at St-Hyacinthe region of Quebec (45° 37' 00" 72° 57' 00"). Individuals of the three species were kept in laboratory and fed with an artificial diet, black bean aphid *Aphis fabae* Scopoli, commercial crushed pollen and eggs of *Sitotroga cerealella* (Olivier, 1789). at 24 ± 1°C, 16L:8D. Egg of each species were removed individually, incubated at constant conditions, and experimental larvae and pupae were removed when required. All individuals were starved for 24h prior to experiments.

Experiment 1: Intraguild predation between H. axyridis, C. maculata and P. quatuordecimpunctata

IGP experiments were performed in Petri dishes of 50 mm x 9.4 mm containing a moist cotton rolls in order to keep humidity constant. Experimental pairings, consisting of one individual of each species, was placed in one Petri dish during 24 hrs. This design was replicated 15 times for each combination of instars for the three species (*H. axyridis* vs *C. maculata*, *H. axyridis* vs *P. quatuordecimpunctata* and *P. quatuordecimpunctata* vs *C. maculata*). An IGP event was assessed when consumed individuals were observed. Natural mortality was evaluated in Petri dishes containing only one individual of each species; dead individuals were subtracted to the observed mortality estimates in the IGP experiments. IGP intensity was assessed as the proportion of replicates where IGP occurred. IGP rates were compared for each instar by G-test. Symmetry index was calculated as follows: number of replicates in which a predator was preyed upon/ total number of replicates in which IGP occurred

(Lucas *et al.* 1998; Lucas 2005). This symmetry index was compared by G-test to a 50% theoretical index, that corresponds to a symmetrical interaction (Scherrer 1994).

An additional experiment was carried out to evaluate egg number consumed by each larval or adult individuals of each species. Five eggs were deposited in one Petri dishes and the number consumed recorded after 24h. Egg number consumed by each instar was compared between species with an ANOVA.

All individuals were weighed before the experiment using a Mettler electronic balance. Weight of each larval instar of the three species was compared with an ANOVA. Weight difference between IGpredator and IGprey were calculated for each larval combination for the three species and correlated with IGP intensity (Félix and Soares 2004).

To evaluate if *H. axyridis* is a more efficient intraguild predator, we compare total number of intraguild interactions for three species combinations by a G-test to a 50% theoretical index.

Experiment 2: Indirect sublethal effects

Indirect effects of interference between *H. axyridis* and *C. maculata* were evaluated by survival and weight loss of 3rd instar larval on young corn plants (20 cm height). Observations of attack and escape behaviors were also recorded. Third larval instar of each species was chosen for their similar size and their relative aggressivity (Yasuda *et al.* 2001). Larvae were weighed before and after the experiments and weight loss was compared between species and with weight loss of control individuals held alone on corn plant. Behaviours of 3rd larval instar of both species were observed during 30 minutes and mortality was determined after 4 hours. Number of contacts and attack events were counted. Attack events were defined as contact that elicit a defense by the attacked individual. The attack rate was calculated as the number of individuals attacked divided by the number of individuals contacted and compared with an ANOVA (Yasuda *et al.* 2001). The data were arcsine-square

root transformed before analysis in order to normalize distribution. Defense events were determined as falling off the plant or running away following a contact (escaping). The number of defense events were compared between species by ANOVA.

II. 4 RESULTS

Experiment 1: Intraguild predation between *H. axyridis*, *C. maculata* and *P. quatuordecimpunctata*

IGP between *H. axyridis* and *C. maculata*

IGP was observed between *H. axyridis* and *C. maculata* in 59% of the tests. In total combinations (N = 675), IGP was mutual but significantly asymmetrical in favor of *H. axyridis* was observed, which preyed on CM in 37% of the combinations, while *C. maculata* consumed *H. axyridis* in 21% of the cases (Likelihood ratio G-test; $P < 0.05$) (Figure 1). *Harmonia axyridis* eggs and young instars were consumed by several mobile stages of *C. maculata*, indicating that the species was vulnerable to predation (Figure 1). However, no *H. axyridis* 4th instar and pupae were preyed upon (Figure 1). *H. axyridis* adult and larvae preyed on all mobile and immobile stages of *C. maculata* (Figure 1). Each stage of both species were exclusively either a predator or a prey. In combinations that were significantly asymmetrical, the rate of predation ranged between 35.7 and 100% by *C. maculata* and 46.6 to 100% by *H. axyridis*. The highest value of IGP occurred in combinations with *H. axyridis* 4th instar (69%).

IGP between *H. axyridis* and *P. quatuordecimpunctata*

IGP was observed between *H. axyridis* and *P. quatuordecimpunctata* in 59% of the tests. In total combinations (N = 675), IGP was mutual but significantly asymmetrical in favor of *H. axyridis*, which preyed on P14 in 41% of the cases, while *P. quatuordecimpunctata* consumed *H. axyridis* in 13% of combinations (Likelihood ratio G-test; $P < 0.05$) (Figure 2). Each stages of both species were exclusively either a predator or a prey. *P. quatuordecimpunctata* was able to consume eggs, 1st and 2nd larval instars of *H. axyridis* (Figure 2). However, no 3rd larval instar, 4th larval instar and pupae of *H. axyridis* were preyed upon by *P. quatuordecimpunctata* (Figure 2). All mobile and immobile stages of *P. quatuordecimpunctata* were preyed upon by *H. axyridis* (Figure 2). In combinations that were significantly asymmetric, the rate of

predation ranged between 33.3 to 100% by *P. quatuordecimpunctata* and 86.6 to 100% by *H. axyridis*. All interactions with *H. axyridis* as the IGpredator were significantly asymmetrical. The highest value of IGP occurred in combinations with *H. axyridis* adults (97.5%).

IGP between P. quatuordecimpunctata and C. maculata

IGP was observed between *P. quatuordecimpunctata* and *C. maculata* in 58% of the tests. In total combinations (N = 675), IGP was mutual but significantly asymmetrical in favor of *C. maculata*, which preyed on *P. quatuordecimpunctata* in 35% of the cases, while *P. quatuordecimpunctata* consumed *C. maculata* in 35% of combinations (Likelihood ratio G-test; $P < 0.05$) (Figure 3). When IGP occurred, all stages of *P. quatuordecimpunctata* or *C. maculata* were preyed upon (Figure 3). Symmetrical interactions were observed only when 1st instar of both species preyed upon each other, whereas other stages of both species were exclusively either a predator or a prey. In combinations that were significantly asymmetrical, the rate of predation ranged between 43.8 to 100% by *C. maculata* and 40 to 100% by *P. quatuordecimpunctata*. The highest value of IGP occurred in combinations with *C. maculata* 4th instar (67%).

Egg predation

Coleomegilla maculata consumed globally 3.52 ± 0.22 eggs of *H. axyridis*, while *P. quatuordecimpunctata* instars consumed 3.05 ± 0.23 eggs. First larval instar of *P. quatuordecimpunctata* consumed significantly more eggs of *H. axyridis* than 1st instar *C. maculata* ($F_{1,28} = 10.00$; $P = 0.004$) (Figure 4). Eggs consumed by other larval instars were not significantly different between *C. maculata* and *P. quatuordecimpunctata* ($P > 0.05$). *C. maculata* adults consumed more eggs than *P. quatuordecimpunctata* adults ($F_{1,28} = 24.38$; $P < 0.0001$) (Figure 4). *C. maculata* adults, 4th and 3rd larval instars consumed 96% of the eggs of *H. axyridis*, while 3rd larval instar of *P. quatuordecimpunctata* consumed 92% of the eggs of *H. axyridis*.

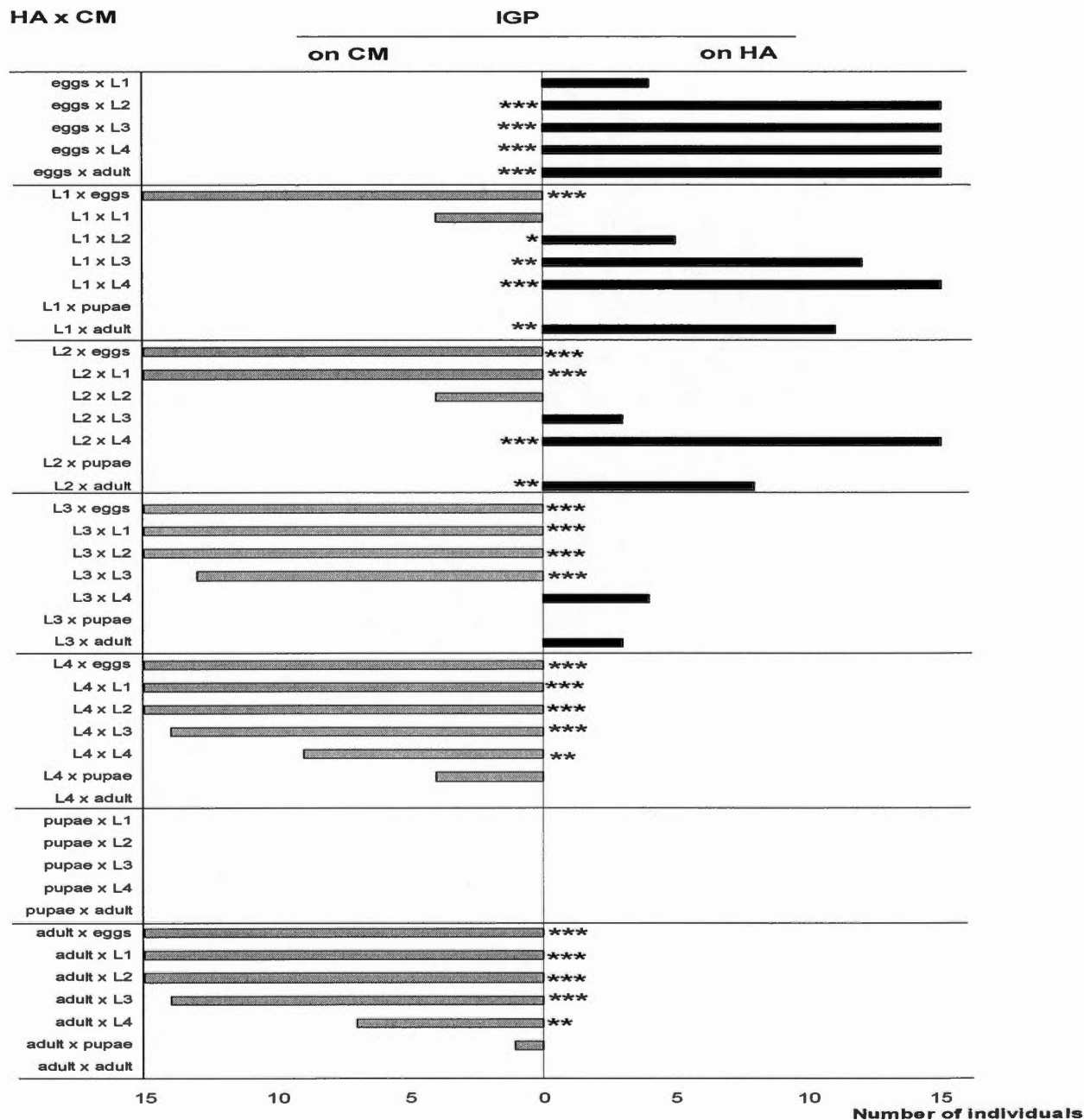


Figure II.1. Intraguild predation (IGP) between *H. axyridis* (HA) and *C. maculata* (CM) in the absence of aphids. The grey bars represent the number of *C. maculata* killed and black bars the number of *H. axyridis* killed. Asterisks represent significant asymmetry for that combinations of predators (χ^2 , $df = 2$, $P < 0.05$). Note: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

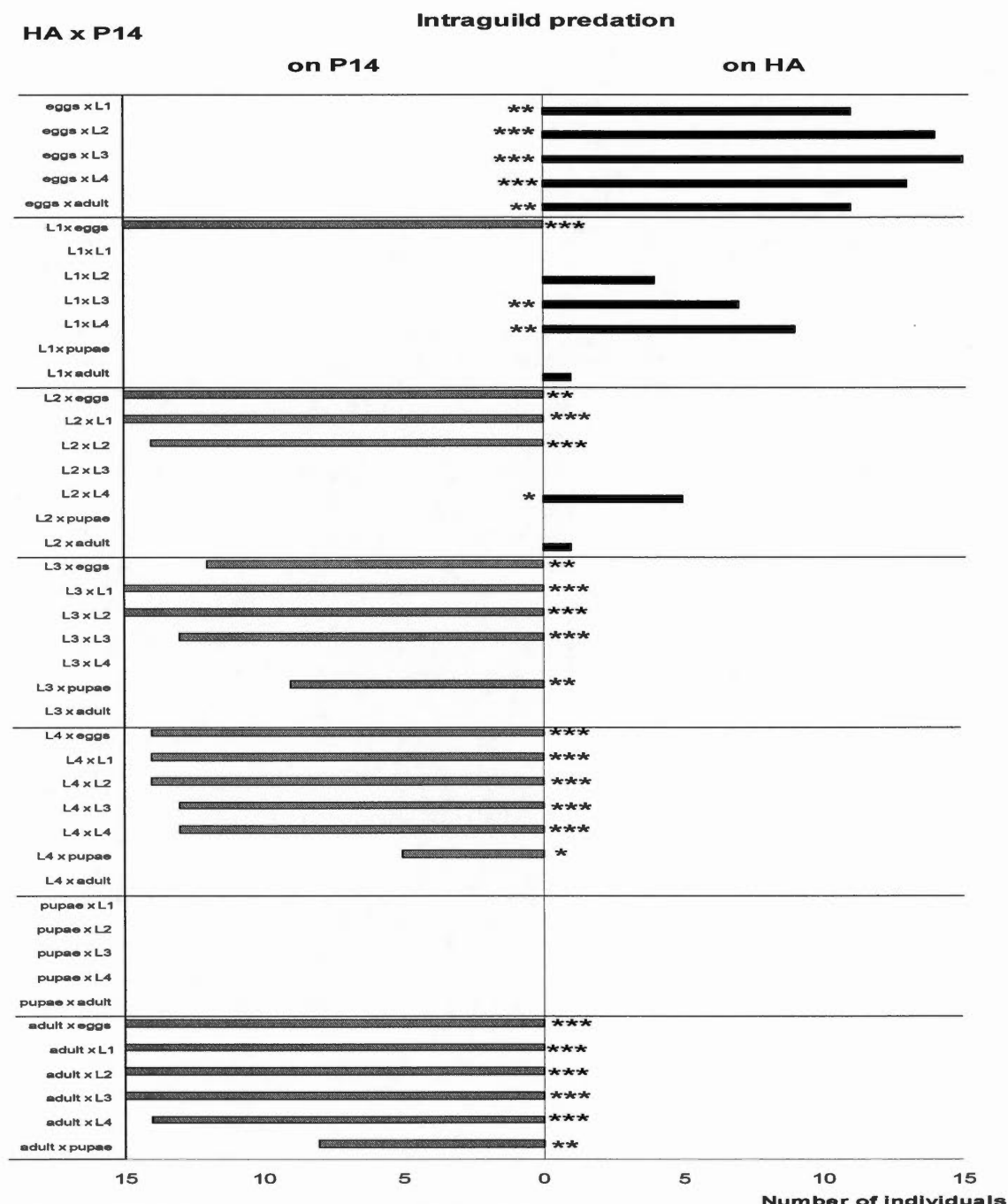


Figure II.2. IGP between *H. axyridis* (HA) and *P. quatuordecimpunctata* (P14) in the absence of aphids. The grey bars represent the number of *P. quatuordecimpunctata* killed and black bars the number of *H. axyridis* killed. Asterisks represent significant asymmetry for that combination of predators (χ^2 , df = 2, $P < 0.05$). Note: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

P14 x CM

Intraguild predation

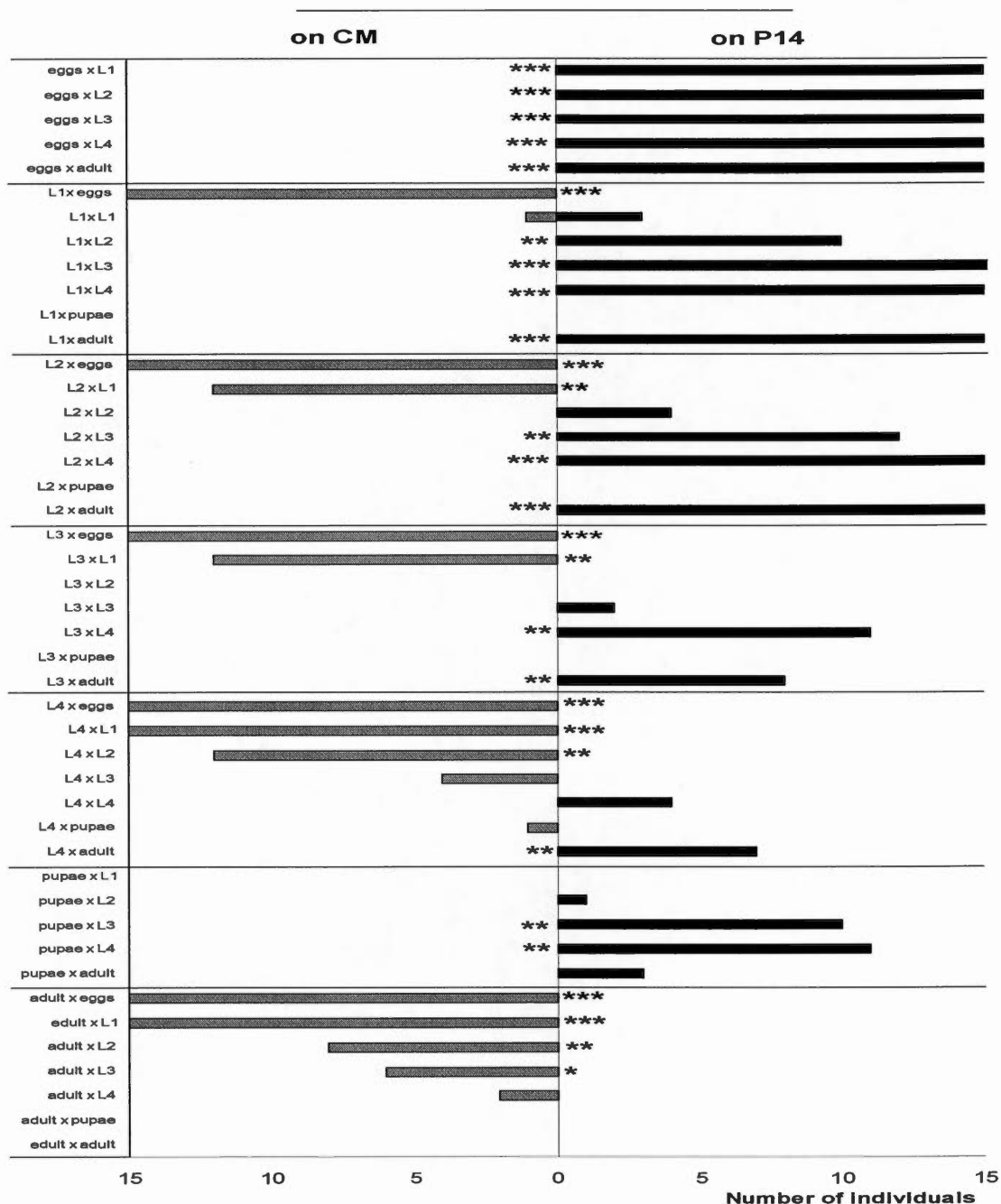


Figure II.3. IGP between *P. quatuordecimpunctata* (P14) and *C. maculata* (CM) in the absence of aphids. The grey bars represent the number of *C. maculata* killed and black bars the number of *P. quatuordecimpunctata* killed. Asterisks represent significant asymmetry for that combinations of predators (χ^2 , df = 2, $P < 0.05$). Note: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

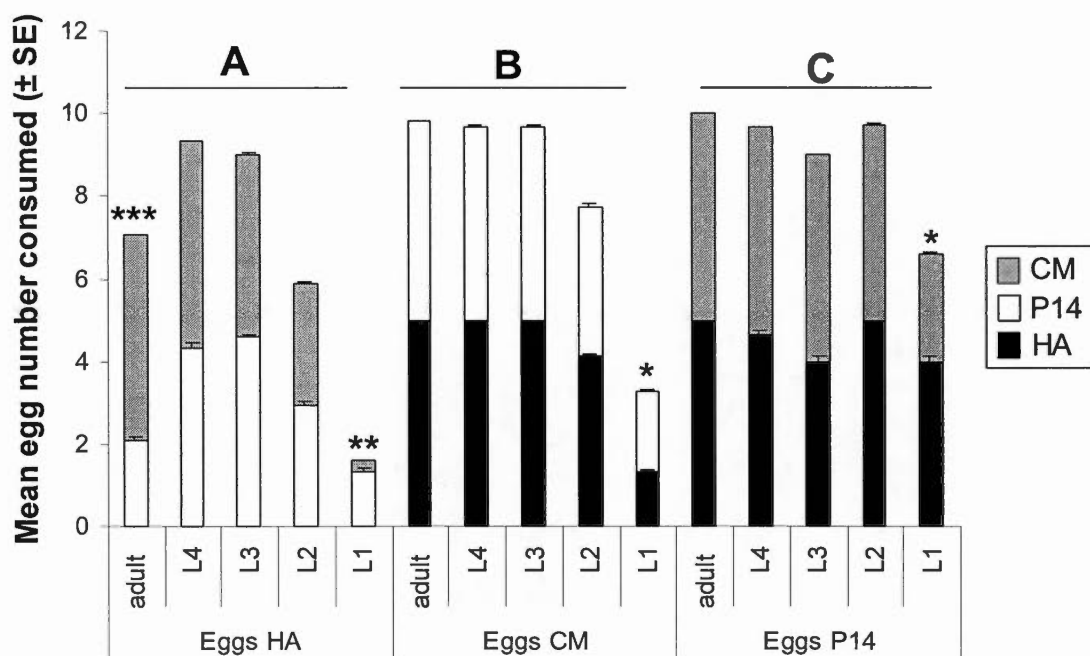


Figure II.4. Number of eggs consumed by the two other ladybeetle species in Petri dishes during 24h. Note: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; indicate differences between species within instars. Different letters indicate differences between species for overall egg consumed by other species.

Harmonia axyridis consumed globally 4.09 ± 0.17 eggs of *C. maculata*, while *P. quatuordecimpunctata* consumed 3.93 ± 0.16 eggs. First larval instar of *P. quatuordecimpunctata* consumed more eggs than 1st larval instar of *H. axyridis* ($F_{1,28} = 7.16$; $P = 0.01$) (Figure 4). Eggs of *C. maculata* were all consumed by adults, 4th and 3rd larval instar of *H. axyridis*, while *P. quatuordecimpunctata* adults, 4th and 3rd larval instars consumed 94.2% eggs of *C. maculata*.

Harmonia axyridis consumed globally 4.54 ± 0.16 eggs of *P. quatuordecimpunctata*, while *C. maculata* consumed 4.47 ± 0.12 eggs. First instar larvae of *H. axyridis* consumed more eggs of *P. quatuordecimpunctata* than 1st larval instar of *C. maculata* ($F_{1,25} = 5.93$; $P = 0.02$) (Figure 4). Eggs of *P. quatuordecimpunctata* were consumed at 90.7% by all instars of *H. axyridis*, while *C. maculata* adults, 4th, 3rd and 2nd larval instars consumed 98.7% eggs of *P. quatuordecimpunctata*.

An overall mean of 4.50 ± 0.10 eggs of *P. quatuordecimpunctata* were consumed by *C. maculata* and *H. axyridis*, significantly higher than *C. maculata* eggs (4.01 ± 0.12) or *H. axyridis* eggs (3.29 ± 0.16) ($F_{2,441} = 22.59$; $P < 0.0001$; Tukey-Kramer test $P < 0.05$) (Figure 4).

Correlation between weight difference and IGP intensity

Weight was similar between first instar larvae of the three species ($F_{5,52} = 0.30$; $P = 0.74$). *Harmonia axyridis* and *C. maculata* 2nd instar were heavier than *P. quatuordecimpunctata* larvae ($F_{2,52} = 22.81$; $P < 0.0001$; Tukey-Kramer test $P < 0.05$). *Harmonia axyridis* 3rd instars ($F_{2,52} = 43.80$; $P < 0.0001$; Tukey-Kramer test $P < 0.05$) and 4th larval instars ($F_{2,52} = 46.83$; $P < 0.0001$; Tukey-Kramer test $P < 0.05$) (Figure 5A) were heavier than *C. maculata* or *P. quatuordecimpunctata*.

Weight differences between larval instars IGpredator and IGprey were calculated and plotted with respective IGP intensity (Figure 5B;C;D). Significant relationships were observed between IGP intensity and weight difference in the

combination *H. axyridis*-*C. maculata* ($R^2 = 0.33$; $F_{1,14} = 7.13$; $P = 0.02$) (Figure 5B) and in the combination *H. axyridis*-*P. quatuordecimpunctata* ($R^2 = 0.31$; $F_{1,14} = 6.17$; $P = 0.03$) (Figure 5C).

Harmonia axyridis as a more efficient intraguild predator

When all interactions were taken into account, interactions between *H. axyridis* and *C. maculata* ($G = 18.49$, $df = 1$, $P < 0.001$) or *P. quatuordecimpunctata* ($G = 50.64$, $df = 1$, $P < 0.001$) was significantly asymmetrical in favor of the invasive species (Figure 6A, B). Interactions between *C. maculata* and *P. quatuordecimpunctata* were significantly asymmetrical in favor of *C. maculata* ($G = 7.26$, $df = 1$, $P = 0.007$) (Figure 6C).

Experiment 2: Indirect sublethal effects

No IGP mortality was observed during 4h experiment on 3rd instar larvae of *C. maculata* and *H. axyridis*.

Sublethal indirect effect of IGP on weight

Harmonia axyridis lost twice ($0.37 \text{ mg} \pm 0.07$) as much weight as *C. maculata* ($0.17 \text{ mg} \pm 0.08$) (Figure 7A), but this difference was not significant ($F_{1,54} = 1.86$; $P = 0.18$). Relative weight loss of *H. axyridis* ($5.6 \pm 1.1\%$) was not different than *C. maculata* ($2.8 \pm 1.5\%$) ($F_{1,54} = 1.17$; $P = 0.28$) (Figure 7B). No differences were observed in weight loss between *C. maculata* in predation experiment and *C. maculata* on control plant ($F_{1,36} = 0.04$; $P = 0.84$) (Figure 7A) or in relative weight loss ($F_{1,36} = 0.24$; $P = 0.63$) (Figure 7B). No differences were observed in weight loss between *H. axyridis* in predation experiment and *H. axyridis* on control plant ($F_{1,36} = 0.15$; $P = 0.70$) (Figure 7A) or in relative weight loss ($F_{1,36} = 0.01$; $P = 0.93$) (Figure 7B).

Observation of behaviors

Predation behaviors were not different between the two species. No differences were observed between *C. maculata* and *H. axyridis* in contact ($F_{1,27} = 2.37$; $P = 0.13$) or attack number ($F_{1,28} = 1.16$; $P = 0.29$). Attack rate was not different between *H. axyridis* ($61.8\% \pm 8.8$) and *C. maculata* ($48.8\% \pm 8.1$) ($F_{1,38} = 1.21$; $P = 0.28$).

Defensive behaviors were mainly of two types: falling off the plant or running away following an attack (escaping). No differences were observed between the two species for falling off the plant ($F_{1,21} = 1.60$; $P = 0.22$) or escaping ($F_{1,22} = 0.24$; $P = 0.63$).

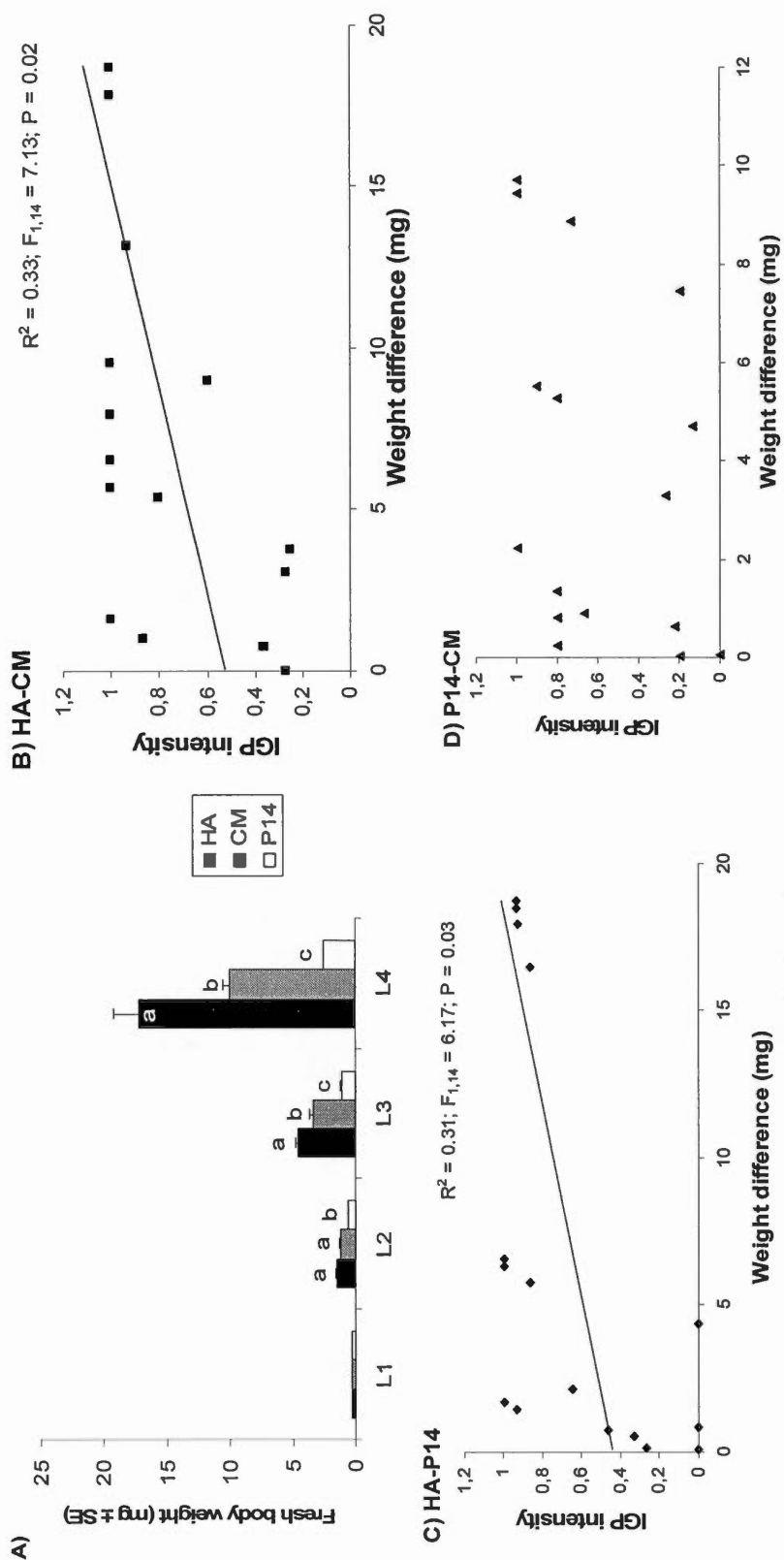


Figure II.5. A) Fresh weight differences between 1st, 2nd, 3rd and 4th larval instars of *H. axyridis* (HA), *C. maculata* (CM) and *P. quatuordecimpunctata* (P14). Different small letters indicate significant fresh body weight differences ($P < 0.05$). B) Relationship between weight difference of the IGpredator and IGprey and IGP intensity of *H. axyridis* and *C. maculata*. C) Relationship between weight difference of the IGpredator and IGprey and IGP intensity of *H. axyridis* and *P. quatuordecimpunctata*. D) Relationship between weight difference of the IGpredator and IGprey and IGP intensity of *P. quatuordecimpunctata* and *C. maculata*.

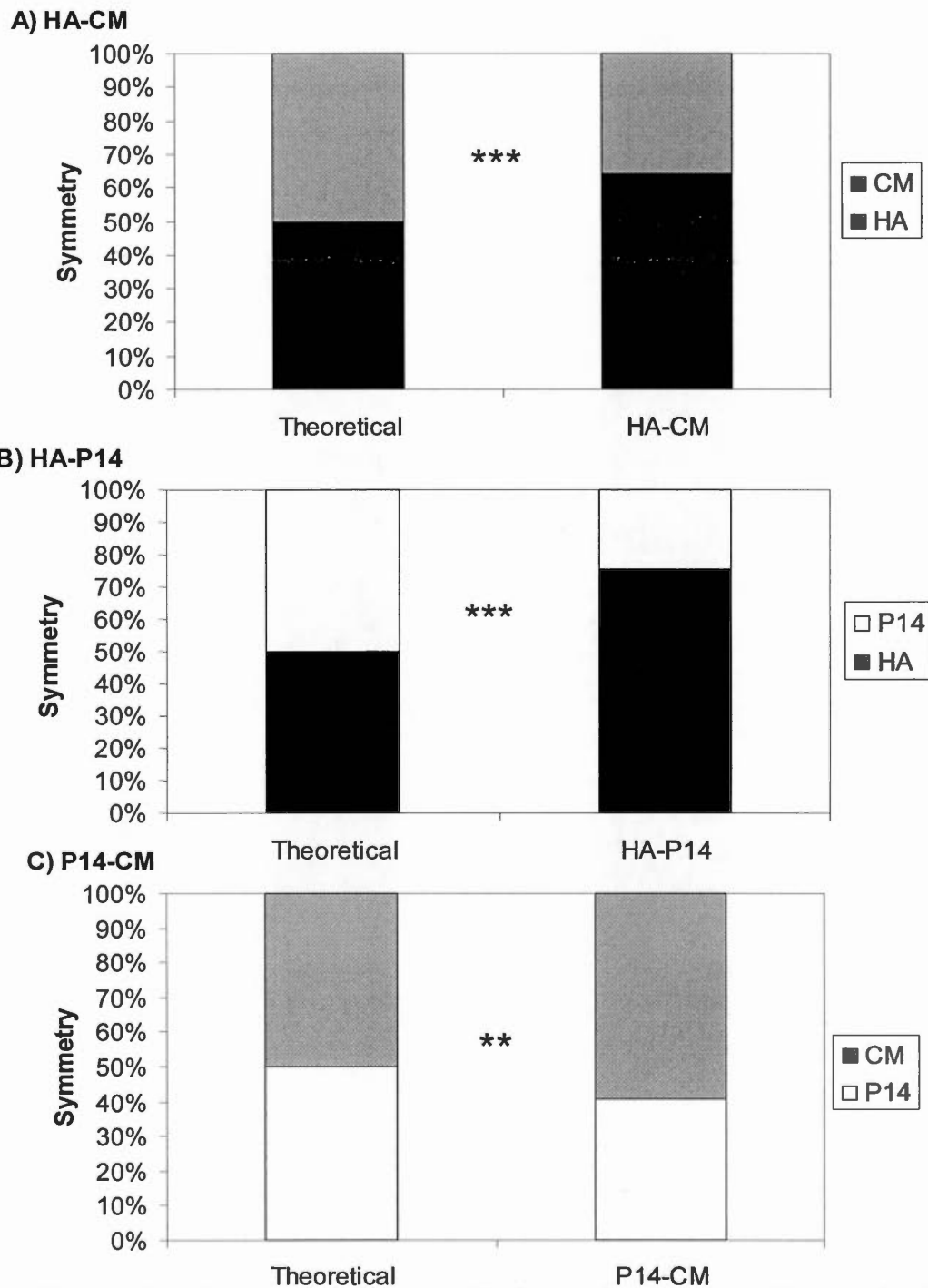


Figure II.6. Symmetry of interspecific interactions between *H. axyridis* (HA), *C. maculata* (CM) and *P. quatuordecimpunctata* (P14) in Petri dishes. Note: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

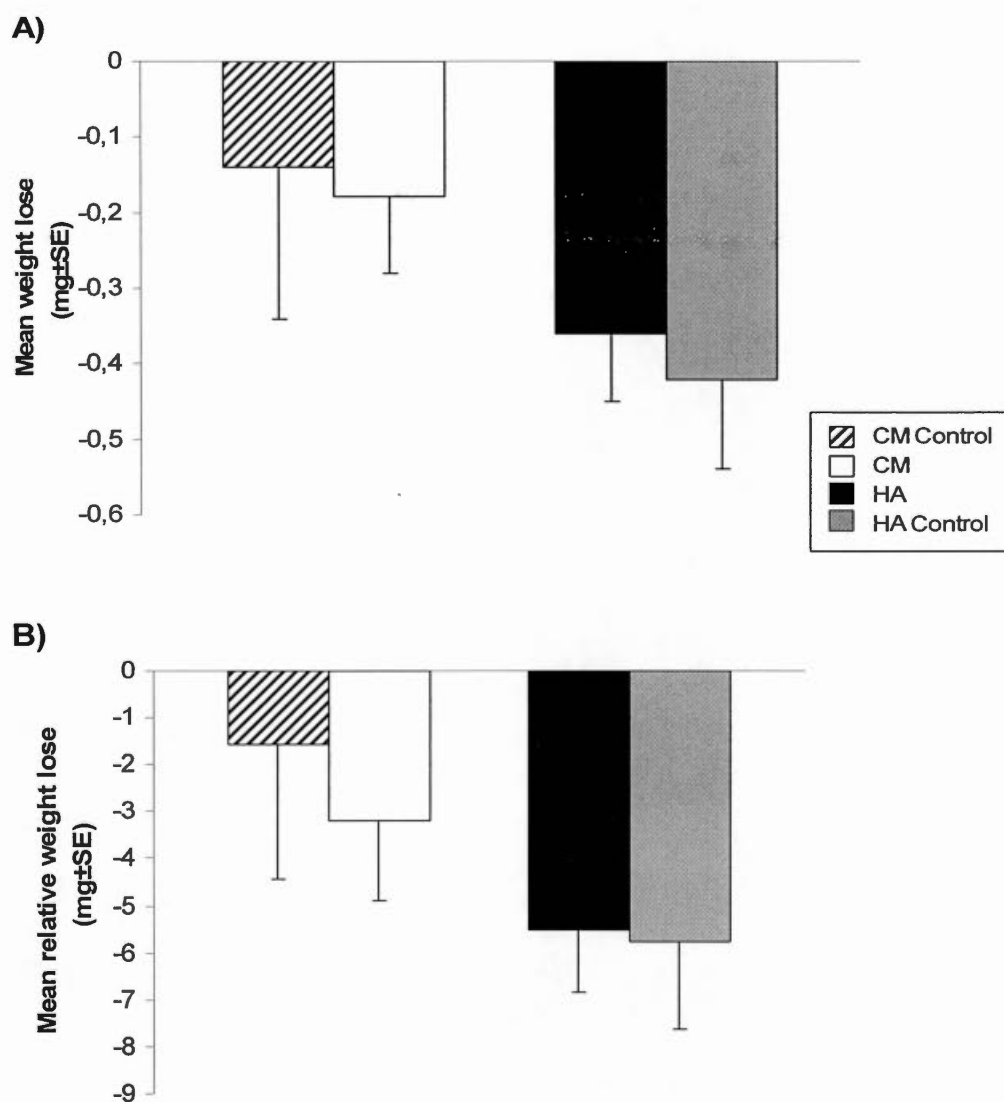


Figure II.7. A) Mean weight loss differences of *H. axyridis* and *C. maculata* alone on corn plants (HA Control, CM Control) or in presence of each other during 4h in absence of aphids (HA or CM). B) Relative mean weight loss (weight loss/weight) of *H. axyridis* and *C. maculata* alone on corn plants (HA Control, CM Control) or in presence of each other during 4h in absence of aphids (HA or CM).

II.5 DISCUSSION

This study demonstrated that *H. axyridis* is a more efficient intraguild predator than either an indigenous and another nonindigenous ladybeetle and that it preyed on all juvenile stages of these two species. However, *H. axyridis* could be an intraguild prey, especially eggs and younger instars, that suggest that *H. axyridis* could be vulnerable to predation in the field. Contrary to our hypotheses, no indirect sublethal effect was observed between *H. axyridis* and *C. maculata* 3rd larval instars on corn plants. The invulnerability of older larval instar and pupal stages to predation and higher efficiency in intraguild interactions could contribute to its invasive success.

At species level, *H. axyridis* was an efficient IG predator, performing asymmetrical interactions in 65% of the cases with *C. maculata* and in 75% of the cases with *P. quatuordecimpunctata* (Figure 6). Furthermore, at individual level, all juvenile stages of *C. maculata* or *P. quatuordecimpunctata* were attacked and consumed by *H. axyridis* (Figure 1, 2). Snyder *et al.* (2004) demonstrated that *H. axyridis* was able to capture and kill larvae of *H. convergens* and *C. transversoguttata* over 70% of the time, whereas as the intraguild prey, it was only captured and killed 25% of the time. Félix and Soares (2004) demonstrated that *H. axyridis* was the IG predator in most combinations with all instars of *C. undecimpunctata*. Our experiment demonstrated also that *H. axyridis* successfully consumed same larval instars of *C. maculata* or *P. quatuordecimpunctata*. The experiments of Cottrell and Yeargan (1998) demonstrated high levels of IGP of *H. axyridis* 2nd instars against *C. maculata* 2nd instars (86.7%) and *H. axyridis* 4th instars on *C. maculata* 4th instars (94.3%) after 24 hr. Our study demonstrated similar results, but to a lesser degree. Thus, *H. axyridis* 2nd instars performed IGP at 26.7% on *C. maculata* 2nd instar, and *H. axyridis* 4th instar consumed successfully *C. maculata* 4th instar in 60% of the time. This experiment, with all stages tested, demonstrate clearly that *H. axyridis* is a more efficient intraguild predator than an indigenous and another invasive ladybeetles. If

our laboratory studies reproduce field behavior, IGP pressure by *H. axyridis* on these two common ladybeetles in our area could explain in part its great invasive success.

Our study demonstrated however that *H. axyridis* was vulnerable to intraguild predation since eggs, 1st and 2nd larval instars were consumed by the two other ladybeetle species (Figure 1, 2 4). Egg predation could be very common in natural systems. Some species avoid laying eggs near aphid colonies to reduce predation by aphidophagous guild (Cottrell 2004; Mills 1982; Agarwala *et al.* 2003). Furthermore, many species chemically deterred their eggs from predation by other coccinellids (Agarwala and Dixon 1992; Hemptinne *et al.* 2000; Sato and Dixon 2004; Sato *et al.* 2005). *Adalia bipunctata* used chemical protection of its eggs against *C. septempunctata*, but chemical protection was ineffective against *H. axyridis* (Sato *et al.* 2005). In our system, between 61 and 85% of eggs were consumed by *C. maculata* and *P. quatuordecimpunctata* in Petri dishes (Figure 1, 2, 4). This indicates that eggs of *H. axyridis* could be vulnerable to predation in the fields and that chemical protection seems ineffective. However, we did not evaluate long term survival on egg diet, and it was demonstrated that other species, such as *C. maculata*, had reduced survival when fed only with *H. axyridis* eggs (Cottrell 2004). Conversely, ladybeetles such as *C. maculata*, *H. axyridis* and *P. quatuordecimpunctata* are polyphagous species that will not feed only on one resource in the field. In the field, *H. axyridis* lays its eggs in presence of older larvae and adult of *C. maculata* (Labrie *et al.* unpublished data) and egg predation in the field could be very common, but the presence of other resources may allow survival, even if eggs are not suitable as a long-term diet. *Harmonia axyridis* first and second larval instar were also very vulnerable to predation, being consumed at 66% and 31% by *C. maculata* and *P. quatuordecimpunctata*, respectively. These results raised some doubt about the status of top-predator that was assigned to this invasive ladybeetle (Dixon 2000). Even if it makes efficient intraguild predation, *H. axyridis* was not protected in our Petri, by chemical protection or behaviors, in eggs and young larval

instars. Its status as a top-predator required further validation with other experiments, as these vulnerable instars are not protected from predation. Coexistence of other species in the field could be possible as eggs and young larvae are susceptible to IGP. Further experiments are however needed to evaluate the strength of the interactions in the field.

By contrast, older instars of *H. axyridis* seems to be well protected from predation. No 4th larval instars were preyed by *C. maculata*, and no 3rd and 4th larval instars by *P. quatuordecimpunctata*. Experiments of Yasuda *et al.* (2001) demonstrated that 3rd and 4th instar were more aggressive than young instars, that could explain reduced IGP rate on these instars. Spines are also well developed in 3rd and 4th larval instar of *H. axyridis*, but not in earlier instars (Koch 2003). The absence of spines could explain high rate of IGP on *H. axyridis* young instars. *Coleomegilla maculata* and *P. quatuordecimpunctata* pupae were also preyed by *H. axyridis*. In counterpart, *H. axyridis* pupae seems to be protected from predation by *P. quatuordecimpunctata* and *C. maculata* because no pupae were consumed during our experiment. Coccinellid pupae stage is usually highly vulnerable to predation. Pupae are immobile over a long time, with few defensive mechanisms other than flicking up and down when something touch it or by chemical defense (Lucas *et al.* 2000). *Coleomegilla maculata* will pupate outside plant, far from aphid colonies, to avoid predation on this vulnerable stage (Lucas *et al.* 2000). Labrie *et al.* (2006) demonstrated that *H. axyridis* pupae take more time to develop in adult than *C. maculata*, potentially increasing its vulnerability to predation. However, in our study, no pupae were preyed upon, either by the indigenous species or by the other invasive species. Experiment of Félix and Soares (2004) demonstrated also that *H. axyridis* pupae were almost invulnerable to IGP. Size, strength of the integument and distastefulness (Félix and Soares 2004), as well as defensive behavior such as flicking up and down, may explain lower vulnerability of the pupal stage of this species. Other studies demonstrated such an invulnerability for chrysopids pupae to IGP by

coccinellids (Lucas *et al.* 1998) and syrphids pupae to IGP by mirids (Fréchette *et al.* 2007). Pupal stage could be less vulnerable to predation then previously thought (Lucas 2005). More studies are however needed to understand this protection of *H. axyridis* pupae. Older larval instar and pupae seems thus less vulnerable to predation, which would give a great advantage in the field, and could explain in part its invasive success.

Many studies refer to the importance of body size in IGP, where in most cases, the difference in size determines the outcome of the interaction, in which smaller individuals are killed by larger ones (Agarwala and Dixon 1992; Félix and Soares 2004; Hindayana *et al.* 2001; Lucas *et al.* 1997, 1998; Obrycki *et al.* 1998; Polis *et al.* 1989; Polis and Holt 1992; Snyder *et al.* 2004; Yasuda *et al.* 2001). Thus, as difference between IGpredator and IGprey will increase, IGP intensity will rise. In this study, this relationship was significant in the two combinations including *H. axyridis* larvae, but not between *P. quatuordecimpunctata* and *C. maculata* (Figure 5 B, C, D). Félix and Soares (2004) demonstrated an increase in IGP intensity by *H. axyridis* on *Coccinella undecimpunctata* with an increase in body weight difference between protagonists. Previous experiment on development demonstrated that *H. axyridis* grow more rapidly to 3rd larval instar than *C. maculata* (Labrie *et al.* 2006), suggesting that rapid growth to less vulnerable instar give advantage in intraguild interactions. Furthermore, a 5th larval instar, with similar developmental time to the 4th larval instar, and bigger than other individuals, was observed in some cases in this experiment. It may be interesting to verify if increased difference in size will lead to increase IGP intensity with these 5th larval instars. Nonetheless, rapid growth to invulnerable instar and increase of IGP intensity with size could be advantageous during the invasion of this species.

Indirect sublethal effects of IGP are rarely assessed in IGP experiments (Lucas 2005). Evaluation of IGP in a system more complex than Petri dishes -like plants-, and with similar size larvae allow evaluation of some indirect effects. Our

experiment with 3rd larval instar of *C. maculata* and *H. axyridis* on corn plant did not however demonstrate any direct or indirect effects. No mortality by IGP was observed between *H. axyridis* and *C. maculata* on corn plants during 4 hours. We expected however some indirect effects on weight between control and IGP situation. Yasuda and Kimura (2001) showed that development of the young larvae of *H. axyridis* and *C. septempunctata* was slowed in presence of the crab spider *Misumenops tricuspidatus* (Fabricius), while older larvae of *H. axyridis* were not affected. Third larval instar could thus be less vulnerable to indirect sublethal effect of IGP. However, relative weight loss in 4h was relatively important, ranging from 3 to 6% of their weight (Figure 7). These results could indicate that the presence of an intraguild predator imposes a similar stress than the lack of food. In the field, IGP will not arise during a long time because when individual escape after an attack, by falling off the plant for example, it will have good chances to survive. In laboratory experiments, individuals are usually confined in small arenas during 24h and mortality is probable, as individuals have to eat some food after just few hours to survive and no escape is possible, as our experiments demonstrated. Our experiments showed that in short term interactions with similar size ladybeetle, no IGP was observed and coexistence is thus possible. More studies are however needed to evaluate indirect effects on long-term experiments.

Decision to attack or not another individual could influence their survival (Lima and Dill 1990; McPeck 2004). Many contacts and attacks were observed between *H. axyridis* and *C. maculata* on plants. The advantage of relative IGP among *H. axyridis* and *C. maculata* or *P. quatuordecimpunctata* may be determined also by behavioural and defensive differences not related to size. Experiments by Snyder *et al.* (2004) suggest that *H. axyridis* both attack more successfully and escape more frequently through a combination of strongly adhesive tarsi and an effective chemical defense. In our experiment, attack rate of *H. axyridis* was not significantly different than *C. maculata*, but slightly higher (68 and 49% respectively). Yasuda *et al.* (2001)

quantified attack rate of *H. axyridis* and *C. septempunctata*, to evaluate the cause of difference IGP incidence. They found that *H. axyridis* had an attack rate exceeding 50%, while *C. septempunctata* had a 20% average rate. Our results could indicate that IGP could be reduced with these similar attack and escape rate. However, our experiment was done only on 3rd larval instar, with similar size. IGP could be in favour of *H. axyridis* in presence of younger instars, with less efficient defensive mechanisms (Yasuda *et al.* 2001). *Harmonia axyridis* 3rd instar successfully escaped from the attacks of *C. maculata* and vice versa. However, in some cases, *H. axyridis* was held a dozen of seconds by *C. maculata*, and escaped only after wriggling. Once, an attack by *C. maculata* on *H. axyridis* led to one spines of *H. axyridis* stuck on labium of *C. maculata*, resulting in its escape while *C. maculata* paused to remove this spine with legs. Differences in morphology in several insects species sometimes function as a mechanism preventing capture by a predator (Yasuda *et al.* 2001; Michaud and Grant 2003). *Harmonia axyridis* seems to be protected from IGP by its aggressive behaviours and by its spineous morphology (Dixon 2000; Michaud and Grant 2003).

There is no doubt that *H. axyridis* can impose a serious threat to indigenous species (see Lucas *et al.* Annexe B). Many field observations reported some decrease in indigenous ladybeetle species following *H. axyridis* arrival (Brown and Miller 1998; Colunga-Garcia and Gage 1998; Tedders and Schaefer 1994; Michaud 2002; Reitz and Trumble 2002; Snyder *et al.* 2004). However, this species is not invulnerable (as a top-predator have to be); coexistence with local species is possible. *Harmonia axyridis* eggs are vulnerable to predation, and other species can eat 1st and 2nd instars. Our experiment performed on plant demonstrated that more complex system could reduce IGP between same size larvae, and that coexistence between the native and this invasive species might be possible. Our study confirmed however that great predation abilities could explain in part the invasive success of *H. axyridis*. Other characteristics of this ladybeetle, such as rapid development, presence of a 5th

larval instar (Labrie *et al.* 2006), capacity to overwintering in human houses, and lack of influence of environmental characteristics such as productivity, along with great predation abilities may contribute to its invasive success in many area of the world.

II.6 ACKNOWLEDGEMENTS

We thank Fanie Courchesne, Isabelle Desjardins and Janick Durocher for their technical assistance. Special thanks to Bruno Fréchette and Nathalie Roullé for revision of an earlier draft of the manuscript. This research was supported by an NSERC scholarship granted to G. Labrie, and NSERC grants to D. Coderre and E. Lucas.

II.7 REFERENCES

- Adriaens, T., Branquart, E. and Maes, D. (2003) The multicolored asian ladybird *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), a threat for native aphid predators in Belgium? *Belgian Journal of Zoology*, **133**, 195-196.
- Agarwala, B. K. and Dixon, A. F. G. (1992) Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecological Entomology*, **17**, 303-309.
- Agarwala, B. K., Yasuda, H. and Kajita, Y. (2003) Effect of conspecific and heterospecific feces on foraging and oviposition of two predatory ladybirds: role of fecal cues in predator avoidance. *Journal of Chemical Ecology*, **29**, 357-376.
- Alyokhin, A. and Sewell, G. (2004) Changes in a lady beetle community following the establishment of three alien species. *Biological Invasions*, **6**, 463-471.
- Arim, M. and Marquet, P.A. (2004) Intraguild predation: a widespread interaction related to species biology. *Ecology Letters*, **7**, 557-564.
- Bando, K. J. (2006) The roles of competition and disturbance in a marine invasion. *Biological Invasions*, **8**, 755-763
- Brown, M. W. and Miller, S. S. (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News*, **109**, 143-151.
- Burgio, G., Santi, F. and Maini, S. (2002) On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). *Biological Control*, **24**, 110-116.
- Coderre, D., Lucas, E. and Gagné, I. (1995) The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) in Canada. *Canadian Entomologist*, **127**, 609-611.

- Colautti, R. I., Bailey, S. A., van Overdijk, C. D. A., Amundsen, K. and MacIsaac, H. J. (2006) Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions*, **8**, 45-59.
- Colunga-Garcia, M. and Gage, S. H. (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology*, **27**, 1574-1580.
- Corbin, J.D. and D'Antonio, C.M. (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology*, **85**, 1273–1283.
- Cottrell, T. E. (2004) Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biological Control*, **31**, 362-371.
- Cottrell, T. E. and Yeargan, K. V. (1998) Intraguild predation between an introduced lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Journal of Kansas Entomological Society*, **71**, 159-163.
- Dawson, M. (2002) Plant quarantine: a tool for preventing the introduction and spread of alien species harmful to plants. In: Claudi, R., Nantel, P. and Muckle-Jeffs, E. (eds) *Alien Invaders in Canada's Waters, Wetlands and Forests*, pp 243–251. Canadian Forest Service, Ottawa, Canada
- Day, W. H., Prokrym, D. R., Ellis, D. R. and Chianese, R. J. (1994) The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera, Coccinellidae) in the United States, and thoughts on the origin of this species and 5 other exotic lady beetles in Eastern North-America. *Entomological News*, **105**, 244-256.
- de Almeida, L. M. and da Silva, V. B. (2002) Primeiro registro de *Harmonia axyridis*

- (Pallas) (Coleoptera, Coccinellidae): um coccinelídeo originário da região Palearctica. *Revista Brasileira Zoológica*, **19**, 941-944.
- Dixon, A.F.G. (2000) Insect predator-prey dynamics : ladybird beetles and biological control. Cambridge University Press, Cambridge, 257 pp.
- Dudgeon, S.R., Steneck, R.S., Davison, I.R. and Vadas, R.L. (1999) Coexistence of similar species in a space-limited intertidal zone. *Ecological Monographs*, **69**, 331–352.
- Elliott, N., Kieckhefer, R. and Kauffman, W. (1996) Effects of an Invading Coccinellid On Native Coccinellids in an Agricultural Landscape. *Oecologia*, **105**, 537-544.
- Ellis, D.R., Prokrym, D.R. and Adams, R.G. (1999) Exotic lady beetle survey in northeastern United States: *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Entomological News*, **110**, 73-84.
- Evans, E. W. (2004) Habitat displacement of North American ladybirds by an introduced species. *Ecology*, **85**, 637-647.
- Félix, S. and Soares, A. O. (2004) Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of body weight. *European Journal of Entomology*, **101**, 237-242.
- Fox, T.B., Landis, D.A., Cardoso, F.F. et Difonzo, C.D. (2005) Impact of predation on establishment of the soybean aphid, *Aphis glycines* in soybean, *Glycine max*. *BioControl*, **50**, 545-563.
- Fréchette, B. Rojo, S., Alomar, O. et Lucas, E. (2007) Intraguild predation between syrphids and mirids : Who is the prey ? Who is the predator? *BioControl*, **52**, 175-191.

- Gordon, R. D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of New York Entomological Society*, **93**, 1-912.
- Hemptinne, J. L., Lognay, G., Gauthier, C. and Dixon, A. F. G. (2000) Role of surface chemical signals in egg cannibalism and intraguild predation in ladybirds (Coleoptera : Coccinellidae). *Chemoecology*, **10**, 123-128.
- Hindayana, D., Meyhöfer, R., Scholz, D. And Poehling, H.-M. (2001) Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. *Biological Control* **20**, 236-246.
- Hironori, Y. and Katsuhiko, S. (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga*, **42**, 153-163.
- Holt, R. D. and Polis, G. A. (1997) A Theoretical framework for intraguild predation. *American Naturalist*, **149**, 745-764.
- Hoogendoorn, M. and Heimpel, G. E. (2004) Competitive interactions between an exotic and a native ladybeetle: a field cage study. *Entomologia Experimentalis et Applicata*, **111**, 19-28.
- Kajita, Y., Takano, F., Yasuda, H. and Agarwala, B. K. (2000) Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. *Applied Entomology and Zoology*, **35**, 473-479.
- Kiesecker, J. M., Blaustein, A. R. and Miller, C. L. (2001) Potential mechanisms underlying the displacement of native red-legged frogs by introduced bullfrogs. *Ecology*, **82**, 1964-1970.
- Koch, R. L. (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of*

Insect Science, **3**, 1-16.

- Labrie, G., Lucas, E. and Coderre, D. (2006) Can developmental and behavioral characteristics of the multicolored Asian lady beetle *Harmonia axyridis* explain its invasive success? *Biological Invasions*, **8**, 743-754.
- LaMana, M. L. and Miller, J. C. (1996) Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biological Control*, **6**, 232-237.
- Lima, S.L. and Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.
- Lodge, D. M., Williams, S. L., MacIsaac, H. J., Hayes, K., Leung, B., Reichard, S., Mack, R. N., Moyle, P. B., Smith, M., Andow, D. A., Carlton, J. T. and McMichael, A. (2006) Biological invasions: recommendations for U.S. policy and management. Position paper of the Ecological Society of America., 71 p.
- Lucas, E. (2005) Intraguild predation among aphidophagous predators. *European Journal of Entomology*, **102**, 351-364.
- Lucas, E. and Brodeur, J. (1999) Oviposition site selection by the predatory midge *Aphidoletes aphidimyza* (Diptera : Cecidomyiidae). *Environmental Entomology*, **28**, 622-627.
- Lucas, E., Coderre, D. and Brodeur, J. (1998) Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology*, **79**, 1084-1092.
- Lucas, E., Coderre, D. and Brodeur, J. (2000) Selection of molting and pupation sites by *Coleomegilla maculata* (Coleoptera: Coccinellidae): avoidance of intraguild predation. *Environmental Entomology*, **29**, 454-459.

- Lucas, E. and Alomar, O. (2002a) Impact of *Macrolophus caliginosus* presence on damage production by *Dicyphus tamaninii* (Heteroptera: Miridae) on tomato fruits. *Journal of Economic Entomology*, **95**, 1123-1126.
- Lucas, E. and Alomar, O. (2002b) Impact of the presence of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on whitefly (Homoptera: Aleyrodidae) predation by *Macrolophus caliginosus* (Wagner) (Heteroptera: Miridae). *Biological Control*, **25**, 123-128.
- Lucas, E., Labrie, G., Vincent, C. and Kovach, J. (in press) The multicoloured Asian lady beetle *Harmonia axyridis* – beneficial or nuisance organism? In Vincent, C., Goettel, M. And Lazarovitz, G. (eds.) Case studies in biological control : a global perspective. CABI Publishing, UK.
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. and Bazzaz, F. A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control [Review]. *Ecological Applications*, **10**, 689-710.
- Majerus, M., Strawson, V. and Roy, H. (2006) The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. *Ecological Entomology*, **31**, 207-215.
- McPeck, M. A. (2004) The growth/predation risk trade-off: so what is the mechanism? *American Naturalist*, **163**, E88-E111.
- Michaud, J. P. (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. *Environmental Entomology*, **31**, 827-835.
- Michaud, J. P. and Grant, A. K. (2003) Intraguild predation among ladybeetles and a green lacewing: do the larval spines of *Curinus coeruleus* (Coleoptera: Coccinellidae) serve a defensive function? *Bulletin of Entomological Research*, **93**, 499-505.

- Mignault, M.-P., Roy, M. et Brodeur, J. (2006) Soybean aphid predators in Québec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *BioControl*, **51**, 89-106.
- Mills, N. J. (1982) Voracity, cannibalism and coccinellid predation. *Journal of Applied Biology*, **101**, 144-148.
- Musser, F. R. and Shelton, A. M. (2003) Factors altering the temporal and within-plant distribution of coccinellids in corn and their impact on potential intraguild predation. *Environmental Entomology*, **32**, 575-583.
- Nault, B. A. and Kennedy, G. G. (2003) Establishment of multicolored Asian lady beetle in Eastern North Carolina: seasonal abundance and crop exploitation within an agricultural landscape. *BioControl* **48**, 363-378.
- Obrycki, J. J., Giles, K. L. and Ormord, A. M. (1998) Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia* **117**, 279-285.
- Okuyama, T. (2002) The role of antipredator behavior in an experimental community of jumping spiders with intraguild predation. *Population Ecology* **44**, 121-125.
- Park, Y.-L. and Obrycki, J.J. (2004) Spatio-temporal distribution of corn leaf aphids (Homoptera: Aphididae) and ladybeetles (Coleoptera: Coccinellidae) in Iowa cornfields. *Biological Control* **31**, 210-217.
- Pervez A. and Omkar (2006) Ecology and biological control application of multicoloured Asian ladybird, *Harmonia axyridis*; a review. *Biocontrol Science and Technology* **16**, 111-128.
- Phoofolo, M. W. and Obrycki, J. J. (1998) Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. *Entomol. Exp. Appl.* **89**, 47-55.

- Pimentel, D., Lach, L., Zuniga, R. and Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**, 53-65.
- Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. and Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment* **84**, 1-20.
- Polis, G. A. and Holt, R. D. (1992) Intraguild predation: the dynamics of complex trophic interactions. *TREE* **7**, 151-154.
- Polis, G. A., Myers, C. A. and Holt, R. D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Ann. Rev. Ecol. Syst.* **20**, 297-330.
- Provost, C., Coderre, D., Lucas, É. and Bostanian, N. J. (2003) Impact of lambda-cyhalothrin on intraguild predation among three mite predators. *Environmental Entomology* **32**, 256-263.
- Reitz, S. R. and Trumble, J. T. (2002) Competitive displacement among insects and arachnids. *Annual Review of Entomology* **47**, 435-465.
- Saini, E.D. (2004) Presencia de *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) en la provincia de Buenos Aires. Aspectos biológicos y morfológicos. *Ria* **33**, 151-160.
- Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N. and Weller, S. G. (2001) The population biology of invasive species. *Annual Review of Ecology & Systematics* **32**, 305-332.
- San Martin, G., Adriaens, T., Hautier, L. and Ottart, N. (2005) La coccinelle asiatique

Harmonia axyridis. *Insectes* **136**, 7-11.

- Sato, S. and Dixon, A. F. G. (2004) Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. *Agricultural and Forest Entomology* **6**, 21-24.
- Sato, S., Yasuda, H. and Evans, E. W. (2005) Dropping behaviour of larvae of aphidophagous ladybirds and its effects on incidence of intraguild predation: interactions between the intraguild prey, *Adalia bipunctata* (L.) and *Coccinella septempunctata* (L.), and the intraguild predator, *Harmonia axyridis* Pallas. *Ecological Entomology* **30**, 220-224.
- Scherrer, B. (1984) Biostatistique. Gaëtan Morin. Chicoutimi, Québec, Canada.
- Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *TREE* **17**, 170-176.
- Simberloff, D. (2005) The politics of assessing risk for biological invasions: the USA as a case study. *Trends in Ecology and Evolution* **20**, 216-222.
- Snyder, W. E., Clevenger, G. M. and Eigenbrode, S. D. (2004) Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia* **140**, 559-565.
- Tedders, W. L. and Schaefer, P. W. (1994) Release and establishment of *Harmonia axyridis* (Coleoptera, Coccinellidae) in the southeastern United-States. *Entomological News* **105**, 228-243.
- Turnock, W. J., Wise, I. L. and Matheson, F. O. (2003) Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. *Canadian Entomologist* **135**, 391-404.
- Wheeler, A.G. and Hoebeke, E.R. (1995) *Coccinella novemnotata* in northeastern North America: Historical occurrence and current status (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, **97**,

701-716.

Yasuda, H., Kikuchi, T., Kindlmann, P. and Sato, S. (2001) Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior* **14**, 373-384.

Yasuda, H. and Kimura, T. (2001) Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. *Entomologia Experimentalis et Applicata* **98**, 17-25.

Yasuda, H. and Ohnuma, N. (1999) Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia Experimentalis et Applicata* **93**, 63-67.

CHAPITRE III

OVERWINTERING STRATEGY OF THE MULTICOLORED ASIAN LADY BEETLE (COLEOPTERA: COCCINELLIDAE): *COLD-FREE SPACE AS A FACTOR OF INVASIVE SUCCESS*

III.1 ABSTRACT

Successful overwintering of a coccinellid species is partially dependent on quality of hibernacula, for surviving cold temperatures, minimize risk of drowning, and for avoiding parasitism or infection by pathogens. The multicolored Asian ladybeetle *Harmonia axyridis* (Pallas), an introduced species that spread in North America since 1988, overwinter outside and inside houses or man-made structures. Five experiments were conducted during winter 2003-2004 to evaluate winter survival of the invasive *H. axyridis* compared to the indigenous *Coleomegilla maculata lengi* Timberlake outside and inside houses, in order to assess its contribution to the invasive success of the multicolored Asian ladybeetle. We formulated the hypothesis that *H. axyridis* will survive during winter inside houses and that no survival would be observed outside in our area. Survival of *H. axyridis* ranged from 25% to 53% in different experiments inside houses whereas no survival was recorded outside. *Coleomegilla maculata* did not survive inside houses, but 12.5% of the individuals survived outside. The indigenous species *C. maculata* presented higher proportion of lipids than the invasive species, suggesting that *H. axyridis* is not physiologically adapted to overwinter in our country. Selection of houses as overwintering site by the multicolored Asian ladybeetle may constitute a *cold-free space*, which could explain its great invasive success in northern countries.

Key words: overwintering survival, *Harmonia axyridis* Pallas, *cold-free space*, *Coleomegilla maculata lengi*

III.2 INTRODUCTION

In temperate areas, overwintering strategies and survival are important factors that may influence greatly the invasive success of a species. In many insects winter survival is the primary determinant of their future abundance (Bale 1991, Honěk 1989). Choice of overwintering sites could also reduce natural enemies of these insects, such as entomopathogens or parasites that are commonly present on these sites (Honěk 1989). Entomogenous fungi may be present either on individuals that invade hibernacula or in soil of these sites and will infect individuals in spring, when humidity is really high (Ceryngier 2000, Harwood *et al.* 2006, Honěk 1989, Nedved 1993, Riddick and Schaefer 2005, Riddick 2006). Parasitoids in hibernacula may either enter diapause together with their hosts or may promptly develop inside the adult stage in host, which are still not dormant (Ceryngier and Hodek 1996, Hodek 1973). For invasive insects species in temperate areas, overwintering strategies and survival should be a determinant to reach great abundance and reinvade in high density the environment after each winter.

The Palearctic multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) spread rapidly through North America since 1988 (Chapin and Brou 1991, Coderre *et al.* 1995, Colunga-Garcia and Gage 1998, Dreistadt *et al.* 1995, Tedders and Schaefer 1994). This coccinellid species was introduced many times during the last century as a biological control agent of aphids and scales (McClure 1987, Tedders and Schaefer 1994). *Harmonia axyridis* was first observed in Canada in 1994 (Coderre *et al.* 1995) and is now widely distributed throughout this province (Lucas *et al.* 2002, Lucas *et al.* Annex A), as far as 48° latitude (Labrie, personal observation).

In Asia, this species overwinter in crevices in rock or in concrete objects like buildings and sometimes in leaf litter (Obata 1986, Sakurai *et al.* 1993). The species show an hypsotactic aggregation, e.g. is connected with prominent isolated and contrasting objects visually present in relatively dry situation (Obata 1986, Obata *et*

al. 1986, Nalepa *et al.* 2005, Sakurai *et al.* 1992) and hibernacula are found in the same place every year (Obata 1986). In Japan, the second or third generation of *H. axyridis* aggregates at overwintering sites in early November and adults enter reproductive diapause before winter, decrease their respiration rate and accumulate glycogen and lipids (Sakurai *et al.* 1992). The adults emigrate to breeding sites in late March (Obata 1986, Osawa 2001). *Harmonia axyridis* accumulate myoinositol also as a cryoprotectant and is considered as a freeze intolerant species that change its supercooling ability seasonally (Koch *et al.* 2004, Somme 1982, Watanabe 2002). Experiments had shown that this species is paralyzed at -5°C, with an optimum overwintering temperature between 0°C and -5°C and a great mortality occurred at -20°C (Watanabe 2002).

In North America, the most obvious overwintering sites of the multicolored Asian lady beetle are houses or other man-made structures, where they can constitute a nuisance for human beings (Hagley 1999, Huelsman *et al.* 2001, Kidd and Nalepa 1995, Kovach 2004, LaMana and Miller 1996, Lucas *et al.* Annex B, McCutcheon and Scott 2001, Nalepa *et al.* 1996, Riddick *et al.* 2000, 2004, Schaefer 2003, Yarbrough *et al.* 1999). A study of encaged lady beetles in Connecticut (USA) (McClure 1987) reported more than 90% overwintering mortality the first year and 100% mortality the next year, suggesting that low winter temperatures may be an important factor regulating populations of *H. axyridis* from one year to the next. Laboratory experiments have shown that the supercooling point of adult of this species in United States ranged from -12°C to -16°C (Koch *et al.* 2004). Thus, the species cannot survive prolonged freezing below -16°C in this country. The capacity of *H. axyridis* to survive winter conditions in northern locations may be more related to the availability of quality overwintering sites than to its capacity to increase cold hardiness (Koch *et al.* 2004).

The objective of this study was to evaluate the overwintering strategies of *H. axyridis* in northern region of North America as a contribution to its invasive success.

We hypothesized that the multicolored Asian lady beetle increases its survival by overwintering in human houses. We chose to compare overwintering survival of *H. axyridis* with that of an ecologically similar indigenous species *Coleomegilla maculata lengi* Timberlake. Observations of the invasive species at overwintering sites of this indigenous species have been reported in autumn (Lucas, personal observation).

III.3 MATERIAL AND METHODS

Five experiments were conducted in Southeastern Canada (Québec province) during winter 2003-2004 inside and outside houses to assess overwintering survival of *H. axyridis* and *C. maculata*. Specimens of *H. axyridis* were collected on exterior wall of houses (72°42'W, 45°23'N) when they aggregated in mass in October and November 2003. Specimens of *C. maculata* were collected beneath leaf litter in November 2003 on an overwintering site under willow *Salix nigra* Marsh. (72°56'W, 45°39'N), where thousands of them hibernate year after year. *Harmonia axyridis* individuals were also observed on these sites, on the bark of trees or in the leaf litter (Lucas, pers. observation). Both species were kept one week in incubator at 10°C with water until the commencement of experiments.

Experiment 1: Winter survival outside

One hundred individuals of *H. axyridis* and *C. maculata* were marked with white paint on one elytra and deposited on three overwintering sites of *C. maculata* (N = 300) (72°56'W, 45°39'N; 72°97'W, 45°28'N; 72°92'W, 45°35'N) where individuals of *H. axyridis* were often seen in autumn. These sites were under big trees (willow *S. nigra*; poplar *Populus* sp; maple *Acer saccharum* Marsh.) and under snow cover during most part of winter. Individuals were placed in cavities beneath the leaf litter at the tree base. Temperature during release day in November 2003 was 5°C and 10°C in April 2004. Survival and sex were determined in laboratory and compared between species by likelihood ratio G-test (Sokal and Rohlf, 1995).

Experiment 2: Winter survival in muslin bags in houses

Three closed muslin bags (10 cm x 10 cm) with sterile and dry wooden chips containing 20 coccinellids of *H. axyridis* or *C. maculata* were installed in the basement of three houses (N = 180) (72°42'W, 45°23'N; 73°45'W, 45°28'N; 71°55'W, 45°22'N) in November 2003 and removed in April 2004. Muslin bags were installed on the floor in a corner of the basement, where they could be typically found

(Labrie, personal observation). No food or water were available to the beetles. Temperature and humidity were recorded weekly by electronic thermometer. Survival was recorded in laboratory as ladybeetles walking normally after 24 hr (Watanabe 2002) and sex of the individuals were determined. Differences in survival between species and sex was analysed by likelihood ratio G-test (Sokal and Rohlf 1995).

Experiment 3: Winter survival of *H. axyridis* in Quebec houses

Harmonia axyridis were collected in 15 houses in four regions of Quebec province (74°10'W to 70°98'W; 45°08'N to 46°83'N) (Canada) during one day in March and April 2004. All apparent dead and alive coccinellids were collected and sex of each individual was determined. Temperature and relative humidity inside house during the day of collection were recorded. Survival differences between sexes were determined by chi-squared analysis (Sokal and Rohlf 1995).

Experiment 4: Winter survival in controlled chambers

Six Petri dishes of 10 coccinellids of *H. axyridis* and *C. maculata* with sterile and dry wooden chips were installed in controlled chambers at -5°C and 10°C to the end of November 2003 until April 2004. Relative humidity (RH) was kept constant at 60%, that correspond to the maximal RH found in houses. Two Petri dishes of each species and temperature were removed each month on January to end of March to assess survival and sex. Survival was compared between temperatures and month with likelihood ratio G-test.

Experiment 5: Proportion of lipids

For each of the preceeding four experiments, proportion of lipids on the weight of coccinellids was determined for living individuals. For outside individuals, the measure of proportion of lipids on *C. maculata* were measured on 25 individuals captured on overwintering site in November 2003 and at the beginning of April 2004. This measure were also made on 25 individuals of *H. axyridis* captured outside houses in November and in April around houses. In muslin bags and controlled

chambers, these measures were recorded on live individuals. In Quebec houses, the lipids were extracted for 20 individuals by sites when available. Dry weight was measured with an analytical balance after 48h in a dry oven at 60°C. Lipid weight was determined by the method of Huey (1966) and Zitzman and May (1989). Coccinellids were pierced two times on upper and underside of the abdomen with a fine needle and dried for 48h. They were weighed (dry weight; DW) and put individually in 0.5 ml eppendorf vials in a methanol-chloroforme mixture (2:1) for three days. During this period the solvents dissolved the fats diffusing from the insects. They were removed and dried outside during 24h. They were dried in an oven during another 48h and weighed again (Lean weight; LW). The weight difference obtained determined the lipid weight (DW-LW). The proportion of lipids was calculated as the lipid weight on the lean weight $((DW-LW)/LW)$ for size standardization to eliminate dependency of fresh weight on water and fat (Nedved and Windsor 1994). The proportion of lipids was compared for each independent variables by ANOVA (Sokal and Rohlf 1995). Data of proportion of lipids were transformed by arcsin of squared root (Sokal and Rohlf 1995). All statistical analysis were performed with JMP 5.0[®] (SAS Institute).

III.4 RESULTS

Experiment 1: Winter survival outside

All 300 *H. axyridis* recaptured in April on the three overwintering sites were dead. There was 72 *C. maculata* recaptured in April and nine of these were alive, totalizing $12.5 \pm 5.53\%$ survival. We did not attempt to evaluate survival with total individuals as they could have walked away, be died or not. There was no difference in survival between sites for *C. maculata* ($G = 5.26$; $df = 72$; $P = 0.072$) so data were pooled. Survival was significantly higher for *C. maculata* than *H. axyridis* ($G = 30.52$; $df = 372$; $P < 0.0001$). There was no survival difference between gender for *C. maculata* ($G = 0.51$; $df = 72$; $P = 0.47$).

Experiment 2: Winter survival in muslin bags in houses

Mean relative humidity of houses was 30%, with a temperature fluctuating between 4 and 11°C. There was $24.81\% \pm 3.95$ survival of *H. axyridis* in the muslin bags installed in three heated houses. Survival of *H. axyridis* was not different between houses, so data were pooled. No survival difference were observed between gender for *H. axyridis* ($\chi^2 = 2.18$; $df = 2$; $P = 0.34$). All *C. maculata* in muslin bags inside the three houses were dead before the end of the experiments in April 2004. Survival was higher for *H. axyridis* than *C. maculata* ($\chi^2 = 4.35$; $df = 1$; $P = 0.04$).

Experiment 3: Winter survival of H. axyridis in Quebec houses

During March and April 2004, 2119 *H. axyridis* were collected in 15 houses. Mean survival of *H. axyridis* was $53.0 \pm 6.18\%$. Survival of females was greater than males ($\chi^2 = 106.87$; $df = 1$; $P < 0.0001$) (Figure 1). Temperature in the houses ranged from 7 to 31°C and relative humidity from 25 to 59%.

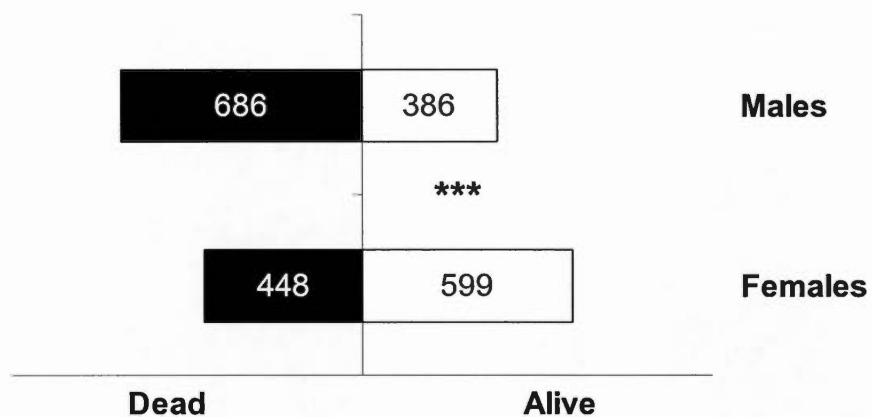


Figure III.1. Survival of females and males of *H. axyridis* collected in 15 houses in Quebec province of Canada during winter 2003-2004. Note: * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Experiment 4: Winter survival in controlled chambers

A significant decrease in survival of *H. axyridis* between months was observed at -5°C ($G = 9.96$; $df = 60$; $P = 0.007$) and 10°C ($G = 60.08$; $df = 58$; $P = 0.0001$) (Figure 2). At the end of winter, 45% of *H. axyridis* individuals had survived at -5°C while no survival at 10°C was reported. Survival was similar at the two temperatures during January ($G = 2.77$; $df = 39$; $P = 0.096$) and February ($G = 2.18$; $df = 40$; $P = 0.14$) but there was higher survival at -5°C in March than at 10°C ($G = 14.61$; $df = 39$; $P = 0.0001$) (Figure 2). No survival difference between males and females *H. axyridis* was observed at -5°C ($G = 0.02$; $df = 59$; $P = 0.90$) or 10°C ($G = 0.08$; $df = 58$; $P = 0.78$) for all months. No individuals of *C. maculata* survived inside controlled chambers at the two temperatures from the beginning of January.

Experiment 5: Proportion of lipids

Outside houses

In November 2003 and in April 2004, there was a greater proportion of lipids for *C. maculata* than *H. axyridis* and for females than males (Table 1; Table 2).

Inside houses

In muslin bags in houses: Proportion of lipids of *H. axyridis* were not different between houses so data were pooled for subsequent analysis. No proportion of lipids differences was observed between gender ($F_{1,41} = 0.06$; $df = 1, 41$; $P = 0.81$) (Table 1).

In Quebec houses: *Harmonia axyridis* females in the 15 houses had a higher proportion of lipid ($F = 4.86$; $df = 1, 221$; $P = 0.029$) than males (Table 1).

Controlled chambers

No differences in proportion of lipids was found between the three months in the two temperatures in incubators, so data were pooled for subsequent analyses.

Proportion of lipids of *H. axyridis* at -5°C were greater than at 10°C (Table 1; Table 2).

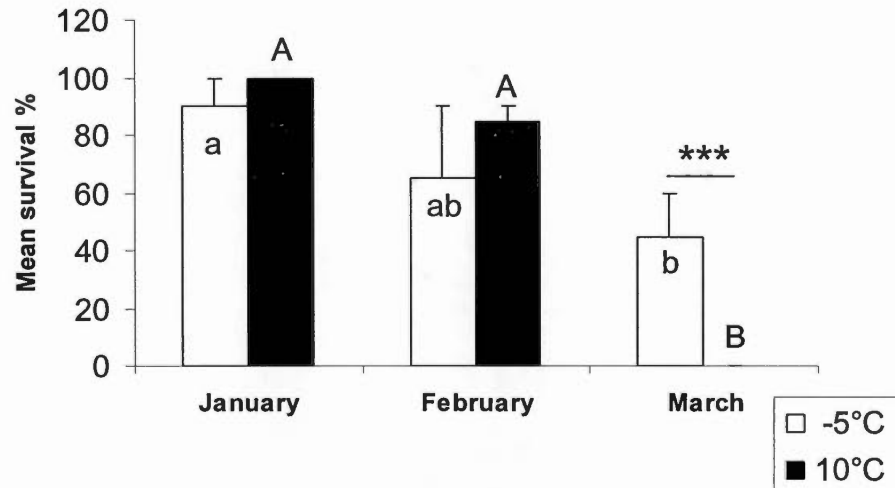


Figure III.2. Survival of *H. axyridis* inside controlled chambers at -5°C and 10°C during winter 2003-2004. Note: Different letters indicate significant differences ($P < 0.05$) between months at -5°C (minuscule letters) and 10°C (capital letters). * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table III.1. Proportion of lipids (%) of females (♀) and males (♂) of *H. axyridis* and *C. maculata* outside houses, inside houses and in controlled chambers during winter 2003-2004.

Experiment	Variables	Species	Proportion of lipids (%) ♀	Proportion of lipids (%) ♂
Outside	Nov.	<i>H. axyridis</i>	35.49 ± 3.30	26.41 ± 3.10
		<i>C. maculata</i>	73.18 ± 5.73	61.40 ± 5.05
Outside	April ¹	<i>H. axyridis</i>	23.95 ± 2.70	16.54 ± 2.08
		<i>C. maculata</i>	56.13 ± 3.18	45.31 ± 6.14
Inside	Muslin bags	<i>H. axyridis</i>	21.06 ± 1.35	22.02 ± 2.49
		<i>C. maculata</i>	-----	-----
Inside	Quebec houses	<i>H. axyridis</i>	21.05 ± 1.10	17.65 ± 0.90
Controlled chambers	-5°C	<i>H. axyridis</i>	46.36 ± 2.58	40.26 ± 4.74
	-5°C	<i>C. maculata</i>	-----	-----
	10°C	<i>H. axyridis</i>	32.73 ± 2.43	28.86 ± 2.75
	10°C	<i>C. maculata</i>	-----	-----

¹ *H. axyridis* individuals were collected outside around houses.

Table III. 2. Analysis of proportion of lipids of *H. axyridis* and *C. maculata* outside houses in November 2003 and April 2004 and in controlled chambers.

Experiment	Effect	df	F	P-level
Outside Nov.	Whole model	3	22.83	<.0001
	Species	1	65.32	<.0001
	Sex	1	5.92	0.021
	Species x Sex	1	0.02	0.89
	Error	31		
Outside April	Whole model	3	27.47	<.0001
	Species	1	74.18	<.0001
	Sex	1	7.57	0.009
	Species x Sex	1	0.006	0.94
	Error	41		
Controlled chambers	Whole model	3	6.51	0.0006
	Temperature	1	13.93	0.0004
	Sex	1	3.14	0.081
	Temperature x Sex	1	0.15	0.70
	Error	71		

III.5 DISCUSSION

We confirmed our hypothesis that *H. axyridis* was unable to survive outside human houses in Southeastern Canada, while the indigenous species *C. maculata* had 12.5% survival. At the opposite, *H. axyridis* survivorship inside houses ranged between 25% to 53% in different trials, whereas no *C. maculata* survived. These results suggest that the invasive success of *H. axyridis* may be linked to a cold-free space selection during winter.

Winter conditions in this northeast part of Canada can stop invasive species that are not morphologically, physiologically or behaviorally adapted to our conditions. Temperatures during winter 2003-2004 ranged between 5°C and -25°C, with 26 days below -15°C, which are normal conditions in our area (Environment Canada 2006). Air temperature above the snow line can be between -20°C and -40°C during winter (Bale 1991). Fluctuating air temperature and snow cover are common and can generate high mortality to overwintering animals (Bale 1991). For example, mortality of *C. maculata* during winter can be quite variable among sites, ranging from 3 to 100% (Benton and Crump 1979, Wright and Laing 1982). The same trend in Europe is observed for *Coccinella septempunctata* L. where mortality ranged from 24% to 100% (Honěk 1997). *Harmonia axyridis* did not survive outside on overwintering sites was observed in our experiments, while *C. maculata* survived at 12.5%. Experiments of Koch et al. (2004) demonstrated that 80% of the *H. axyridis* died when exposed to -15°C and 100% at -20°C after 24h. No winter survival was also observed by McClure (1987) in Connecticut on encaged *H. axyridis* the second year of its experiment. In our experiment, no snow cover was present during some weeks in December and January, with very low temperature, which may explain total mortality of the invasive species. While observed on overwintering sites of *C. maculata*, *H. axyridis* is a species that should better survive in bark crevices or hill top (Hodek and Honěk 1996, Obata 1986, Obata et al. 1986, Sakurai et al. 1992, 1993). Additional observations of the multicolored Asian ladybeetle overwintering on

top of hills near Montreal (Quebec) (73°09'W, 45°18'N; 71°82'W, 45°73'N), showed that individuals observed were dead at the end of winter (Lucas, personal communication).

Conversely, inside houses, temperatures and relative humidity are much more stable during all winter and may provide safe habitat during this period. Human houses could constitute a *cold-free* space for animal species able to exploit them during a part of their life cycle. The indigenous species *C. maculata* was unable to survive inside houses or in controlled chambers in our experiments. These results are in accordance with the experiments of Jean *et al.* (1990), which demonstrated no winter survival of this species at temperatures > 0°C. Relative humidity was also very low in our experiments (ranging from 30 to 60%) and *C. maculata* is known to be very susceptible to desiccation (Benton and Crump 1979, Nedved 1993) and needs 75 to 100% humidity to survive during winter (Jean *et al.* 1990). Conversely, in our two experiments inside houses, we observed survival of *H. axyridis* between 25 and 53%. To our knowledge, only one other coccinellid species, *Adalia bipunctata* L., is known to overwinter in cracks in walls, in lofts, or behind windows and even in rooms of houses, however without comparable use of human houses than *H. axyridis* (Hawkes 1920, Semyanov 1970 in Hodek and Honěk 1996, Majerus 1994, 1997). However, a fair proportion of *A. bipunctata* apparently do not leave natural habitats, orchards, park or forests and hibernate either in crevices of tree, bark or in artificial object or trees (Hodek and Honěk 1996). Our experiments and observations demonstrated that *H. axyridis* was unable to survive outside, suggesting that this behavioral adaptation could be the only way to survive for this species in our area. One question that could be raised by our experiment and will need further investigation, is whether the northern expansion of this species is linked to the presence of man-made structure in the landscape.

Evaluating the populations of *H. axyridis* overwintering inside houses is not an easy task. In rural areas, many houses contained some coccinellids (in terms of

dozen, hundred or thousands of individuals), with higher number in old houses that have more interstices to be invaded (Huelsman *et al.* 2001). Factors such as control by humans, incapacity to find the exit or temperature inside house could also influence the number of individuals reinvading the environment at the end of winter. Our experiments in controlled chambers showed higher survival at the end of winter at -5°C than at 10°C. High mortality at 10°C at the end of winter indicate that *H. axyridis* cannot sustain this temperature more than four to five months. Watanabe (2002) demonstrated that *H. axyridis* individuals survived much longer at 0°C than at 5°C, suggesting that the mortality at higher temperature could be caused by depletion of energy reserves or water rather than by chilling injury. Our evaluation of lipid proportion demonstrate clearly a higher depletion of lipids during winter at 10°C than at -5°C, suggesting that energy reserves are important for survival of *H. axyridis* in heated houses. No studies have attempted to evaluate the impact of these factors on the spring population of *H. axyridis* and more experiments are needed.

Interestingly, females survival was higher than males inside houses. Females showed also higher proportion of lipids than males. It has been demonstrated that in many coccinellid species, females had a higher absolute fat content than males (Hodek and Honěk 1996) and that females are generally larger than males (Nalepa *et al.* 1996, Osawa 2001). In a number of insect species, body size is an important correlate of individual fitness (e.g., Honěk 1997), positively associated with fecundity (Dixon and Guo 1993), flight activity and endurance, resistance to starvation and desiccation, as well as total longevity (Honěk 1997). Nalepa *et al.* (1996) found higher proportion of females of *H. axyridis* in their collection after winter. In our area, overwintering success of females could be due to higher fat content, which provide a food reserve in heated houses. Bazzochi *et al.* (2004) showed that females of *H. axyridis* had a more intense oviposition activity after winter than natives *A. bipunctata* and *Propylea quatuordecimpunctata* Linné. Furthermore, they had the highest post-overwintering rate of increase, that will give a higher capacity to

colonize the environment after winter. Temperature in house in our experiment ranged between 7 to 30°C, with bigger females surviving better than males during hibernation. No such results have been found for the indigenous species, *C. maculata*, where females did not experience higher survival than males. As a consequence, post-overwintering rate of increase could be higher for *H. axyridis*, providing advantages to reinvade the environment after winter, laying eggs in high number and to compete for resources or by interference with other species.

Warm and dry sites could also provide conditions that prevent the spread of disease during the winter (Honěk 1989). While plenty of dead coccinellids were found inside houses, no observations of entomopathogenic fungi mortality on *H. axyridis* was found. Observation of a subsample of 50 *H. axyridis* installed in controlled chambers at 10°C until the end of May (30 d) did not show any effective parasitism or fungal pathogens infection (Labrie, personal observation). It is now crucial to study the survival during winter of parasitoids and fungal pathogens of *H. axyridis* inside house. A differential susceptibility of *H. axyridis* compared to other species to such enemies should influence greatly its invasive success.

The potential northern extension of the distribution of an exotic organism, such as *H. axyridis*, is linked to the capacity of the organism to withstand unfavourable environmental conditions, such as temperature extremes (Tauber *et al.* 1986). Insects in cold regions require some degrees of cold hardiness to protect them from low temperatures (Bale 1987, Salt 1961). As pointed by Koch *et al.* (2004), the cold hardiness of *H. axyridis* in Minnesota and Georgia appears to be a poor predictor of its northern distribution. In our experiment, We demonstrate that the survival of the exotic *H. axyridis* is linked to the selection of human houses by overwintering individuals. Human houses may be considered a *cold-free* space for this species, allowing its geographical extension on north part of North America and contributing to its great invasive success. Our study confirm also the opposite overwintering

strategy of the invasive *H. axyridis* and the indigenous *C. maculata*, indicating a niche differentiation of these two species, and consequently a potential coexistence.

III.6 ACKNOWLEDGMENT

Thanks to homeowners to provide houses and assistance for experiments. Special thanks to Janick Durocher for technical assistance. Thanks to Denis Réale, Onofre Soares, Tim Work and one anonymous referee for suggestions on earlier draft of the manuscript. This research is supported by a NSERC scholarship granted to G. Labrie, NSERC grants to É. Lucas and D. Coderre.

III. 7 REFERENCES

- Bale, J.S. (1987) Insect cold hardiness: freezing and supercooling - an ecological perspective. *Journal of Insect Physiology*, **33**, 899-908.
- Bale, J.S. (1991) Insects at low temperature: a predictable relationship? *Functional Ecology*, **5**, 291-298.
- Bazzochi, G.G., Lanzoni, A., Accinelli, G., and Burgio, G. (2004) Overwintering, phenology and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. *BioControl*, **49**, 245-260.
- Benton, A.H. and Crump, A.J. (1979) Observations on aggregation and overwintering in the coccinellid beetle *Coleomegilla maculata* (DeGeer). *New York Entomological Society*, **87**, 154-159.
- Ceryngier, P. (2000) Overwintering of *Coccinella septempunctata* (Coleoptera: Coccinellidae) at different altitudes in the Karkonosze Mts, SW Poland. *European Journal of Entomology*, **97**, 323-328.
- Ceryngier, P. and Hodek, I. (1996). Enemies of Coccinellidae. In Ecology of Coccinellidae. (eds I. Hodek and A. Honěk), pp. 319-350. Kluwer Academic Publisher, Dordrecht/Boston/London.
- Chapin, J.B. and Brou, V.A. (1991) *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, **93**, 630-635.
- Coderre, D., Lucas, E., and Gagne, I. (1995) The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) in Canada. *Canadian Entomologist*, **127**, 609-611.
- Colunga-Garcia, M. and Gage, S.H. (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology*, **27**, 1574-1580.

- Dixon, A.F.G. and Guo, Y. (1993) Egg and cluster size in ladybird beetles (Coleoptera: Coccinellidae): the direct and indirect effects of aphid abundance. *European Journal of Entomology*, **90**, 457-463.
- Dreistadt, S.H., Hagen, K.S., and Bezark, L.G. (1995) *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae), first Western United States record for this Asiatic lady beetle. *Pan-Pacific Entomologist*, **71**, 135-136.
- Environment Canada. (2006) Climate data online. http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_f.html.
- Hagley, E.A.C. (1999). Predatory insects in fruit orchards in Southern Ontario. Publication 208 Agriculture and Agri-Food Canada and Ontario Ministry of Agriculture, Food and Rural Affairs.
- Harwood, J.D., Ricci, C., Romani, R., Pitz, K.M., Weir, A. and Obrycki, J. (2006) Prevalence and association of the laboulbenialean fungus *Hesperomyces virescens* (Laboulbeniales: Laboulbeniaceae) on coccinellid hosts (Coleoptera: Coccinellidae) in Kentucky, USA. *European Journal of Entomology*, **103**, 799-804.
- Hodek, I. (1973) Biology of Coccinellidae., The Hague, Prague.
- Hodek, I. and Honěk, A. (1996) Ecology of Coccinellidae. Kluwer Academic Publishers, Netherlands.
- Honěk, A. (1989) Overwintering and annual changes of abundance of *Coccinella septempunctata* in Czechoslovakia (Coleoptera, Coccinellidae). *Acta Entomologica Bohemoslovaca*, **86**, 179-192.
- Honěk, A. (1997) Factors determining winter survival in *Coccinella septempunctata* (Col., Coccinellidae). *Entomophaga*, **42**, 119-124.
- Huelsman, M.F., Jasinski, J., Young, C., and Kovach, J. (2001) The multicolored Asian lady beetle *Harmonia axyridis*: a nuisance pest in Ohio.

<http://ipm.osu.edu/lady/icup.htm>.

- Huey, D.H. (1966) Kingzett's chemical encyclopedia: a digest of chemistry and industrial application. William Cloves, London.
- Jean, C., Coderre, D., and Tourneur, J.-C. (1990) Effects of temperature and substrate on survival and lipid consumption of hibernating *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae). *Environmental Entomology*, **19**, 1657-1662.
- Kidd, K.A. and Nalepa, C.A. (1995) Distribution of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in North Carolina and Virginia. *Proceedings of the Entomological Society of Washington*, **97**, 729-731.
- Koch, R.L., Carrillo, M.A., Venette, R.C., Cannon, C.A., and Hutchison, W.D. (2004) Cold hardiness of the multicolored Asian lady beetle (Coleoptera: Coccinellidae). *Environmental Entomology*, **33**, 815-822.
- Kovach, J. (2004) Impact of multicolored Asian lady beetles as a pest of fruit and people. *American Entomologist*, **50**, 159-161.
- LaMana, M.L. and Miller, J.C. (1996) Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biological Control*, **6**, 232-237.
- Lucas, E., Gagné, I., and Coderre, D. (2002) Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **99**, 457-463.
- Lucas, E., Labrie, G., Vincent, C., and Kovach, J. The multicolored Asian ladybeetle, *Harmonia axyridis* - beneficial or nuisance organism? In Case studies in biological control: a global perspective. (eds C. Vincent, M. Goettel and g. Lazarovitz). CABI Publishing, UK. In press.
- Majerus, M.E.N. (1994) Ladybirds Harper Collins, London.
- Majerus, M.E.N. (1997) How is *Adalia bipunctata* (Linn.) attracted to overwintering sites? *Entomologist*, **116**, 212-217.

- McClure, M.S. (1987) Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* bean and godwin (Homoptera: Margarodidae) in the United States. *Environmental Entomology*, **16**, 224-230.
- McCutcheon, T.W. and Scott, H.R. Observation of cosmetic damage on a house caused by the multicolored asian lady beetle, *Harmonia axyridis* (Coleoptera, Coccinellidae). West Virginia University Extension Service.
- Nalepa, C.A., Kidd, K.A., and Ahlstrom, K.R. (1996) Biology of *Harmonia axyridis* (Coleoptera, Coccinellidae) in winter aggregations. *Annals of the Entomological Society of America*, **89**, 681-685.
- Nalepa, C.A., Kennedy, G.G., and Brownie, C. (2005) Role of visual contrast in the alighting behavior of *Harmonia axyridis* (Coleoptera: Coccinellidae) at overwintering sites. *Environmental Entomology*, **34**, 425-431.
- Nedved, O. (1993) Comparison of cold hardiness in two ladybird beetles (Coleoptera: Coccinellidae) with contrasting hibernation behaviour. *European Journal of Entomology*, **90**, 465-470.
- Nedved, O. and Windsor, D. (1994) Supercooling ability, fat and water contents in a diapausing tropical beetle, *Stenotarsus rotundus* (Coleoptera: Endomychidae). *European Journal of Entomology*, **91**, 307-312.
- Obata, S. (1986) Determination of hibernation site in the ladybird beetle, *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae). *Kontyu*, **54**, 218-223.
- Obata, S., Johki, Y., and Hidaka, T. (1986). Location of hibernation sites in the ladybird beetle *Harmonia axyridis*. In Ecology of Aphidophaga. (ed I. Hodek), pp. 193-198. Academia, Prague and Dr. W. Junk., Dordrecht.
- Osawa, N. (2001) The effect of hibernation on the seasonal variations in adult body size and sex ratio of the polymorphic ladybird beetle *Harmonia axyridis*: the

- role of thermal melanism. *Acta Societas Zoologicae Bohemicae*, **65**, 269-278.
- Riddick, E.W. (2006) Influence of host gender on infection rate, density and distribution of the parasitic fungus, *Hesperomyces virescens*, on the multicoloured Asian lady beetle, *Harmonia axyridis*. *Journal of Insect Science*, **6**, available online: insectscience.org/6.42.
- Riddick, E.W., and Schaefer, P.W. (2005) Occurrence, density, and distribution of parasitic fungus *Hesperomyces virescens* (Laboulbeniales: Laboulbeniaceae) on multicoloured Asian lady beetle (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America*, **93**, 1314-1321.
- Riddick, E.W., Aldrich, J.R. et Davis, J.C. (2004) DEET repels *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) adults in laboratory bioassays. *Journal of Entomological Science*, **39**, 373-386.
- Riddick, E.W., Aldrich, J.R., De Milo, A. et Davis, J.C. (2000) Potential for modifying the behavior of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) with plant-derived natural products. *Annals of the Entomological Society of America*, **93**, 1314-1321.
- Sakurai, H., Kawai, T., and Takeda, S. (1992) Physiological changes related to diapause of the lady beetle, *Harmonia axydis* (Coleoptera: Coccinellidae). *Applied Entomology and Zoology*, **27**, 479-487.
- Sakurai, H., Kumada, Y., and Takeda, S. (1993) Seasonal prevalence and hibernating-diapause behavior in the lady beetle, *Harmonia axyridis*. *Research Bulletin of the faculty of Agriculture Gifu University*, **58**, 51-55.
- Salt, R.W. (1961) Principles of insect cold hardiness. *Annual Review of Entomology*, **6**, 55-74.
- Schaefer, P.W. (2003) Winter aggregation of *Harmonia axyridis* (Coleoptera: Coccinellidae) in a concrete observation tower. *Entomological News*, **114**, 23-

28.

- Sokal, R.R. and Rohlf, F.J. (1995) Biometry: the principles and practice of statistics in biological research. 3rd Edition. W. H. Freeman, San Francisco.
- Somme, L. (1982) Supercooling and winter survival in terrestrial arthropods. *Comparative Biochemistry and Physiology, A: Comparative Physiology*, **73**, 519-543.
- Tauber, M.J., Tauber, C.A., and Masaki, S. (1986) Seasonal adaptations of insects. Oxford University Press, New York.
- Tedders, W.L. and Schaefer, P.W. (1994) Release and establishment of *Harmonia axyridis* (Coleoptera, Coccinellidae) in the southeastern United-States. *Entomological News*, **105**, 228-243.
- Watanabe, M. (2002) Cold tolerance and myo-inositol accumulation in overwintering adults of a lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **99**, 5-9.
- Wright, E.J. and Laing, J.E. (1982) Stage-specific mortality of *Coleomegilla maculata lengi* Timberlake on corn in southern Ontario. *Environmental Entomology*, **11**, 32-37.
- Yarbrough, J.A., Armstrong, J.L., Blumberg, M.Z., Phillips, A.E., McGahee, E., and Dolen, W.K. (1999) Allergic rhinoconjunctivitis caused by *Harmonia axyridis* (Asian lady beetle, Japanese lady beetle, or lady bug). *The Journal of Allergy and Clinical Immunology*, **104**, 704-705.
- Zitzman, A.J. and May, M.L. (1989) Growth, food consumption, and nitrogen and lipid composition of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Coccinellidae), as a function of the nitrogen supply of its host plant. *Journal of Entomological Science*, **24**, 62-69.

CHAPITRE IV

IS INVASIVE SUCCESS OF THE MULTICOLORED ASIAN LADYBEETLE *HARMONIA AXYRIDIS* INFLUENCED BY RESOURCE PRODUCTIVITY?

IV.1 ABSTRACT

Invasive species are the second most important cause of biodiversity loss. Identifying the mechanisms resisting and facilitating the establishment of these species is an important goal for ecologists and conservation biologists. Invasive success of a species could be lowered by competition with native species and by resource productivity of the habitat. The multicolored Asian ladybeetle, *Harmonia axyridis* (Pallas), is an invasive species in North America that threatens several indigenous species by competition and intraguild predation. The objectives of this study were to evaluate 1) how resource productivity affect population of *H. axyridis* and a functionally similar indigenous species, *Coleomegilla maculata lengi* Timberlake and 2) how resource productivity affect their coexistence. Experiments were conducted in field cages with corn plants and corn-leaf aphids *Rhopalosiphum maidis* as resources. Three resource levels (100, 250 and 500 aphids) and three combinations of ladybeetles (*H. axyridis* or *C. maculata* single species; *H. axyridis* + *C. maculata*) were introduced in cages. Eggs, larvae, pupae and adults of each species were counted bi-weekly and the number of aphids was kept constant by removing or adding individuals once a week. Observations of intraguild predation and cannibalism were noted. Productivity did not affect the invasive species as supposed: More eggs and larvae of *H. axyridis* were found on lower resource level. However, no differences in adult number, biomass and survival were observed after two months of experiments. Spatial distribution of vulnerable instars however, was affected by resource. Intraspecific competition was stronger than interspecific competition between the two ladybeetles as larvae of *H. axyridis* and *C. maculata* and adults of *C. maculata* were more numerous in the mixed treatment than in the single species treatment. Furthermore, coexistence between the two ladybeetles was observed at all levels of productivity. These effects of resource and competition on the two ladybeetles could be explained by the oviposition strategy of the females, high preference of cannibalism and spatial refugia of vulnerable instars of the two species.

Our results suggest that the invasion of *H. axyridis* will not be hampered by resource productivity of the habitat, and that coexistence with an indigenous species is possible at all productivities.

Key words: biological invasion; productivity, *Harmonia axyridis*, *Coleomegilla maculata*; intraguild predation, cannibalism, oviposition strategy.

IV.2 INTRODUCTION

Invasive species can negatively affect natural ecosystems by disturbing or destroying habitats, spreading novel diseases, displacing or eliminating species through competition, predation or herbivory, and altering native vegetation and fire regimes (Mack *et al.* 2000; Pimentel *et al.* 2005). Given the magnitude of these effects, identifying the processes hampering or promoting the establishment of these species is an important goal for ecologists and conservation biologists (Drake *et al.* 1989; Mack *et al.* 2000; Ricciardi 2004; Simberloff *et al.* 2005). Communities and habitats differ in their susceptibility to invasion (Drake *et al.* 1989; Sakai *et al.* 2001; Shea and Chesson 2002). Within communities, species composition, functional groups present in the community, trophic structure and strength of interactions among trophic levels may interact in ways that buffer some communities against invasion more than others (Lambrinos 2006; Levine and D'Antonio 1999; Sakai *et al.* 2001; Shea and Chesson 2002; Tilman 1999). Habitat invasibility can be influenced by heterogeneity, patchiness, complexity, fragmentation, abiotic conditions and also by productivity (resource level) (Burke and Grime 1996; Mack *et al.* 2000; Marco *et al.* 2002; Von Holle and Simberloff 2005).

Competition within communities may interact with resource levels to affect invasibility (Kiesecker *et al.* 2001; Sakai *et al.* 2001). Population size of species may be lowered with lower resource levels, but reduced resource levels may prevent invasions of exotic species if the resource level falls below some threshold required by the invasive species (Marco *et al.* 2002; Tilman 1999). Invasion will be successful if invaders have a higher resource acquisition rate than that of the resident competitors at the same resource densities (e.g. by having a superior foraging technique) (Shea and Chesson 2002). However, an invader would not be uniformly superior to any resident species, but instead might have a superior response to a particular resource, certain amount of resource, or resources found in certain places or at certain times (Chesson 2000). Studies of productivity or enrichment (increasing

carrying capacity of a prey) have been carried out in ecology mainly on its effects on community structure and ecosystem functioning (Diehl and Feissel 2000). Recently, intraguild predation (IGP) has been included in models of food chain theory (Diehl and Feissel 2000; 2001; Holt and Polis 1997; Mylius *et al.* 2001). Intraguild predation is an extreme case of competition by interference where a predator kills and eats a competitor that uses the same resource (Polis *et al.* 1989). This type of interaction, common in nature (Holt and Polis 1997; Lucas 2005; Polis *et al.* 1989), might be facilitating invasion of *H. axyridis* (Brown and Miller 1998; Hoogendoorn and Heimpel 2004; Michaud 2003; Snyder *et al.* 2004; Yasuda and Ohnuma 1999). However, outcomes of these interactions could be influenced by abundance of resources in the habitat (Holt and Polis 1997; Lucas *et al.* 1998; Mylius *et al.* 2001).

Few studies have examined how IGP is influenced by resource level and how it affects coexistence between exotics and indigenous species (Müller and Brodeur 2002). Theory supposed that the trade-off in systems with IGP works to promote coexistence as follows. As in simple competition theory, the more efficient resource exploiter reduces the resources below the point at which the inferior exploiter can reproduce. Without a trade-off, this would drive the inferior exploiter to extinction. Coexistence can occur in systems with IGP because the inferior exploiter uses the more efficient exploiter or 'intraguild prey', as a second resource. But the outcome of this interaction is dependent upon productivity (resource abundance level) (Holt and Polis 1997). Theory predicts that only the intraguild prey species will persist at low productivity because it can successfully produce progeny on fewer resources, while the intraguild predator will drive the intraguild prey to extinction at high productivity because of the numerical response of the IGpredator (Holt and Polis 1997). Thus, at high productivities, IGpredators tend to be sustained at sufficiently high abundance to exclude the IGprey (Holt and Polis 1997). Some theoretical studies supported by empirical data have demonstrated that 1) species that are better in competition by exploitation will have higher survival when productivity is low; 2) that species with

higher intraguild predation or interference competition abilities will have higher survival when productivity is high; and 3) that coexistence is possible when the productivity is intermediate (Balciunas and Lawler 1995; Bohannan and Lenski 1999; Mylius *et al.* 2001; Morin 1999; Diehl and Feissel 2000; 2001). Alternative stable equilibria, mediated by size refugia of one species or via priority effects, may also be possible at intermediate resource level (Chase 1999). Alternative stable equilibria seem particularly likely if there is a strong asymmetry in the benefit the IGpredator receives from consuming the IGprey and the mortality it inflicts on the IGprey (Holt and Polis 1997). Spatial and temporal variations in resources can also lead to coexistence between invasive and native species if there are interspecific trade-offs in the ability of species to exploit resource-rich vs resource-poor patches (Kotler and Brown 1988; Hanski 1989).

The invasion of the multicolored Asian ladybeetle *Harmonia axyridis* Pallas in North America is threatening native coccinellid species by intraguild predation (Firlej *et al.* 2005; Hoogendoorn and Heimpel 2004; Lucas *et al.* Annexe B), but the coexistence with these species seems possible in certain conditions (Brown 2003; Musser and Shelton 2003). This coccinellid species was introduced many times since 1916 in United States (Teddars and Schaefer 1994; Colunga-Garcia and Gage 1998; Brown and Miller 1998) for the purpose of biological control of aphids (McClure 1987; Lucas *et al.* Annexe B; Pervez and Omkar 2006). It appears only in 1988 in Louisiana that *H. axyridis* was successfully installed (Teddars and Schaefer 1994). In 1994, there was the first appearance of this species in Quebec, Canada (Coderre *et al.* 1995; Lucas *et al.* 2002), and the species is now well established in the province south of 48° parallel (Lucas *et al.* Annexe A). The indigenous ladybeetle *Coleomegilla maculata lengi* Timberlake is functionally similar to *H. axyridis* in that they use the same food resources and share a similar spatial and temporal distribution, and thus, impact of *H. axyridis* on population of *C. maculata* could be envisaged (Musser and Shelton 2003; Hoogendoorn and Heimpel 2004; Park and Obrycki 2004;

Labrie *et al.* unpublished data). Few experiments have evaluated environmental characteristics that could reduce invasion success of this lady beetle (Hoogendoorn and Heimpel 2004; With *et al.* 2002). Fragmented landscape reduces search success and foraging of *H. axyridis* on pea aphids in clover crops (With *et al.* 2002). Hoogendoorn and Heimpel (2004) evaluated in a short experiment the effect of low and high aphid densities on the 1st larval instar of *H. axyridis* and *C. maculata* in field cages and recovered more larvae of the two species after one week in high aphid densities, but failed to show competition between the two species. Experiments in cages at low and high aphid abundance with *C. maculata* and *Coccinella septempunctata* L. demonstrated that at low aphid abundance, *C. maculata* was able to survive while *C. septempunctata*, a bigger species and more efficient intraguild predator than *C. maculata*, did not survive, indicating that *C. maculata* was a better resource exploiter (Obrycki *et al.* 1998). No studies have evaluated on a long term experiment the influence of productivity on the invasive success of *H. axyridis* and on further coexistence with indigenous species.

In this paper, the impact of resource levels, aphid abundance, was addressed experimentally on functionally similar ladybeetle species, the invasive species *H. axyridis* and the indigenous species *C. maculata* in corn field of Quebec, Canada. Two hypotheses were tested: (1) How resource levels affect population variables (egg, larvae, pupae and adult number, egg-laying time, developmental time, survival) of *H. axyridis* and *C. maculata*. Lower abundance of *H. axyridis* than *C. maculata* is expected at lower productivity. (2) How resource levels affect the coexistence of *H. axyridis* and *C. maculata* in mixed treatment. Following theory, extinction of *H. axyridis* is expected at low productivity, extinction of *C. maculata* is expected at high productivity and coexistence should be possible at intermediate productivity.

IV.3 MATERIAL AND METHODS

Study site and manipulated species

Adults of *H. axyridis* and *C. maculata* were collected in the St-Hyacinthe region of Quebec (45° 37' 00", 72° 57' 00"). Individuals of the two species were kept in the laboratory on an artificial diet, pea aphid *Acyrtosiphon pisum* Harris, pollen and eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) at constant conditions of $24 \pm 1^\circ\text{C}$ with 16L:8N prior to the experiment. Corn plants were planted individually and allowed to grow in incubators at 25°C and 65% RH until they were planted in cages at the end of June. Two corn plants were planted and encaged in a muslin cage of 1,5 x 1,0 x 2,0m with a velcro closure on one side in a field at L'Assomption, Quebec, Canada (45° 47' 00", 73° 27' 00"). These cages eliminated access to all herbivores and carnivores during all experiment. The cages do not appear to significantly alter the abiotic environment experienced by the animals. Twelve cages separated by 5 meters were installed in 3 rows 10 meters apart. When tassels were present on all the plants and shedding was over in August, corn-leaf aphids, *Rhopalosiphum maidis* Fitch, were installed on the plants.

Experimental design

We used a 3 x 3 factorial design with the following treatments: 1) *H. axyridis* single species; 2) *C. maculata* single species and 3) *H. axyridis* + *C. maculata*. There was also control cages with aphids and no ladybeetles. Three levels of corn aphids, low, medium and high, corresponding to 100, 250 and 500 aphids by cages were randomly installed in the cages (Schellhorn and Andow 1999). Aphid numbers were within the range observed in the field (Labrie *et al.* unpublished data). Each treatment and productivity were replicated 3 times (Spiller and Schoener 1994), for a total of 36 cages. Aphids were counted two times per week and the resource level of each cage was kept constant by removing or adding aphids once a week. No aphids were

removed or added in control cages, but aphid number was counted as in other treatments.

Species manipulation and data collection

In August, six young and naive gravid females of each species (Fréchette *et al.* 2004) were introduced to the cages with treatment « single species » and three gravid females of *C. maculata* and three of *H. axyridis* were introduced in the mixed cages. Females were removed two days after the first observation of the presence of eggs in the cages, to reduce cannibalism and intraguild predation on eggs and young instars.

Population variables

During our biweekly visits, we censused individual number of eggs, larvae, pupae and subsequently adults of the ladybeetles. Observations of each cage took 15 minutes per visit. When all pupae of a cage emerged as adults, these individuals were removed, sexed and weighed. Egg-laying time (time taken by females to lay eggs) and developmental time (time between first eggs seen and first adult emerged) were noted. Survival proportion for each cages was calculated as adult number at the end of experiment divided by egg number at the beginning of experiment.

Spatial niche of vulnerable stages

Position of eggs, larvae and pupae of ladybeetles were recorded for each cage on plants or elsewhere in the cages. Position on the plants were separated in four parts: lower leaves, i.e. leaves under the ear; ear: ears and leaves of the ear; higher leaves: leaves above the ear and under tassel; Tassel and Outside (not on plant). Aphids were counted and their position on the plants were also noted.

Intra- and interspecific interactions

During each biweekly observation, cannibalism (CNB) and intraguild predation (IGP) incidents were noted and an index of relative cannibalism was calculated as number of CNB event observed/number of larvae in the cage.

Statistical analyses

Egg, larvae, pupae and adult number of ladybeetles in each cage were analysed separately by species with repeated measures ANOVA with resource (Low, Medium, High) and heterospecific combination (single species or mixed) as factors and time as repeated variable. Tukey-Kramer tests were performed subsequently to determine precisely the differences between resource or heterospecific combination for each population variables. Data were divided by six for the single species treatment and by three for the mixed treatment, in order to compare population variables for one female of each species. Adult fresh weight was analysed separately for each species by two-way ANOVA with resource and competition as variables. Egg-laying time, developmental time and survival proportion of each species were analysed by two-way ANOVA with resource and competition. Survival proportion was transformed by arcsin of squared root prior to analyses (Sokal and Rohlf 1995). Prior to the analyses, data were checked for equal variances and normality and were transformed when necessary.

Spatial distribution of ladybeetle eggs, larvae and pupae were analyzed using a χ^2 test for likelihood ratios. Pairwise comparisons were conducted between resources levels within species, between competition within species and between species in mixed treatment. Bonferroni corrections were applied to each results to avoid type II error and they were significant if $P < 0.017$ (Sokal and Rohlf 1995).

Number of CNB events were compared between resource and competition using a Wilcoxon test for each species separately. Index of relative CNB were transformed by arcsin squared root and ANOVAs were used to evaluate the effect of resource and competition on the two species separately.

IV.4 RESULTS

For convenience, results are presented in separate sections for resources effect and heterospecific combination effects. Within each section, we present these effects on population variables (egg, larvae, pupae and adult number for each female introduced), biomass and spatial distribution of *H. axyridis* and *C. maculata* separately. Overall statistical analysis results of population variables however are presented in Table 1 and mean population variables in single species and mixed treatment in Table 2.

Effects of resource level in the single species treatment

Effects of resource level on population variables

Harmonia axyridis eggs and larvae were more numerous at low resource level than in medium or high level (Table 1; Figure 1A, B). An interaction between time and resource level was observed on larvae number; more larvae were found at low level than at medium or high level during 2nd week (Figure 2A). First larval instar were more numerous at all resource level than other larval instars ($F_{3,440} = 21.50$, $P < 0.0001$) (Figure 2B).

No effect of resource was observed on pupae or on adult number of *H. axyridis* (Table 1; Table 2; Figure 1C; 1D). However, there was an effect of time and resource on pupae number (Table 1); more pupae were found at low resource level during week 5 (Tukey-Kramer test, $P < 0.05$).

Egg-laying time ($F_{2,36} = 2.36$, $P = 0.10$) and developmental time ($F_{5,12} = 1.19$, $P = 0.37$) of *H. axyridis* were the same for all resource level (Table 2, single species). Survival proportion was similar between resource level ($F_{5,12} = 1.97$, $P = 0.16$) (Table 2, single species).

There was no effect of resource level on egg and adult number of *C. maculata* (Table 1; Figure 1A; D). There was, however, an effect of resource on larvae during

time, which were more numerous at medium resource level than at high or low resource level the 2nd week (Table 1; Figure 2C). More pupae were observed at high resource level than at low or medium levels (Table 1; Figure 1C).

Egg-laying time ($F_{5,12} = 0.96$, $P = 0.48$) and developmental time ($F_{5,10} = 0.18$, $P = 0.96$) of *C. maculata* were similar between resource level (Table 2, single species). Survival proportion was not different between resource level ($F_{5,12} = 0.18$, $P = 0.96$) (Table 2, single species).

Effect of resource level on adult fresh biomass

No effect of resource level was observed on adult biomass of *H. axyridis* ($F_{5,77} = 1.09$, $P = 0.37$) or of *C. maculata* ($F_{5,42} = 0.91$, $P = 0.48$) (Table 2, single species).

Effect of resource level on spatial distribution

Spatial distribution of eggs and pupae of *H. axyridis* differed among resource level. Eggs were laid mostly outside plants at low resource level compared to medium or high level ($G_{6,717} = 163.74$, $P < 0.0001$) (Figure 3). Pupae were distributed outside plants at low resource level compared to medium or high level ($G_{8,172} = 52.55$, $P < 0.0001$).

Egg spatial distribution of *C. maculata* was different between resource level ($G_{4,311} = 92.60$, $P < 0.0001$) (Figure 3). While eggs were laid on ear of corn plants at low and medium resource level, no eggs were found at this place at high level (Figure 3). Too few data were collected on pupae distribution of *C. maculata* and no analyses were conducted.

In the single species cages, corn-leaf aphids, *R. maidis*, were distributed mainly on ear of plants (Figure 3).

Table IV.1. Repeated measures ANOVA on egg, larvae, pupae and adult number of *H. axyridis* and *C. maculata* by resource level (Low, Medium, High) and Heterospecific combination (Single species or Mixed) during 7 weeks of observation.

Source of variation	Value	Exact F	NumDF	DenDF	Prob>F	Value	Exact F	NumDF	DenDF	Prob>F
	<i>H. axyridis</i>					<i>C. maculata</i>				
Egg number										
Between subjects										
Resource	0.19	3.29	2	35	0.05	0.05	0.84	2	34	0.44
Heterospecific combination	0.02	0.72	1	35	0.40	0.01	0.32	1	34	0.57
Resource x Heterospecific combination	0.09	1.62	2	35	0.21	0.01	0.09	2	34	0.92
Within subjects										
Time	3.71	5.82	14	22	0.0001	1.94	2.91	14	21	0.01
Time x Resource	0.26	1.51	28	44	0.11	0.45	0.73	28	42	0.80
Time x Heterospecific combination	0.58	0.91	14	22	0.56	0.51	0.76	14	21	0.70
Time x Resource x Heterospecific combination	0.41	0.88	28	44	0.63	0.60	0.44	28	42	0.99
Larvae number										
Between subjects										
Resource	0.19	9.89	2	104	0.0001	0.07	2.50	2	69	0.09
Heterospecific combination	0.05	5.05	1	104	0.03	0.10	7.09	1	69	0.01
Resource x Heterospecific combination	0.05	2.37	2	104	0.10	0.03	1.06	2	69	0.35
Within subjects										
Time	1.04	6.77	14	91	<.0001	2.19	8.76	14	56	<.0001
Time x Resource	0.53	2.43	28	182	0.0002	0.50	1.67	28	112	0.03
Time x Heterospecific combination	0.24	1.59	14	91	0.10	0.44	1.78	14	56	0.07
Time x Resource x Heterospecific combination	0.70	1.29	28	182	0.16	0.70	0.77	28	112	0.78
Pupae number										
Between subjects										
Resource	0.006	0.09	2	32	0.91	0.50	4.00	2	16	0.04
Heterospecific combination	0.02	0.53	1	32	0.47	0.003	0.05	1	16	0.82
Resource x Heterospecific combination	0.03	0.41	2	32	0.67	0.09	0.71	2	16	0.51
Within subjects										
Time	3.68	4.99	14	19	0.0008	6.30	1.35	14	3	0.46
Time x Resource	0.16	2.06	28	38	0.02	0.08	0.54	28	6	0.88
Time x Heterospecific combination	1.39	1.88	14	19	0.10	1.69	0.36	14	3	0.92
Time x Resource x Heterospecific combination	0.16	2.01	28	38	0.02	0.11	0.43	28	6	0.94
Adult number										
Between subjects										
Resource	0.03	0.80	2	59	0.45	0.08	2.37	2	59	0.10
Heterospecific combination	0.05	2.70	1	59	0.11	0.12	6.80	1	59	0.01
Resource x Heterospecific combination	0.02	0.72	2	59	0.49	0.02	0.67	2	59	0.52
Within subjects										
Time	1.09	3.59	14	46	0.0005	1.03	3.39	14	46	0.0009
Time x Resource	0.55	1.13	28	92	0.33	0.61	0.93	28	92	0.56
Time x Heterospecific combination	0.14	0.47	14	46	0.94	0.29	0.94	14	46	0.52
Time x Resource x Heterospecific combination	0.79	0.42	28	92	0.99	0.70	0.65	28	92	0.90

Table IV.2. Population variables (by females) of the invasive *H. axyridis* and the indigenous *C. maculata* in single species and mixed cages at all resource levels combined.

	<i>H. axyridis</i>			<i>C. maculata</i>	
	Single species	Mixed		Single species	Mixed
Egg number	12.17 ± 4.55	18.88 ± 6.02		8.43 ± 1.95	10.16 ± 1.59
Larvae number	7.17 ± 1.91	13.81 ± 6.27	*	2.25 ± 0.48	3.33 ± 0.48
Pupae number	5.57 ± 1.92	2.95 ± 0.95		1.87 ± 0.74	2.0 ± 1.03
Adult number	2.02 ± 0.45	2.59 ± 0.48		1.43 ± 0.37	2.22 ± 0.37
Egg-laying time	11.89 ± 2.09 days	14.56 ± 3.09 days		16.22 ± 2.80 days	14.22 ± 3.12 days
Developmental time	24.89 ± 2.25 days	25.22 ± 4.45 days		28.5 ± 0.78 days	28.75 ± 4.54 days
Adult fresh biomass	28.9 ± 1.20 mg	31.58 ± 1.63 mg		10.4 ± 1.54 mg	11.63 ± 0.80 mg
Survival proportion	8.02 ± 1.59%	13.58 ± 3.34%		9.82 ± 3.27%	7.80 ± 1.60%

* indicate significant differences between single species and mixed cages as presented in Table 1.

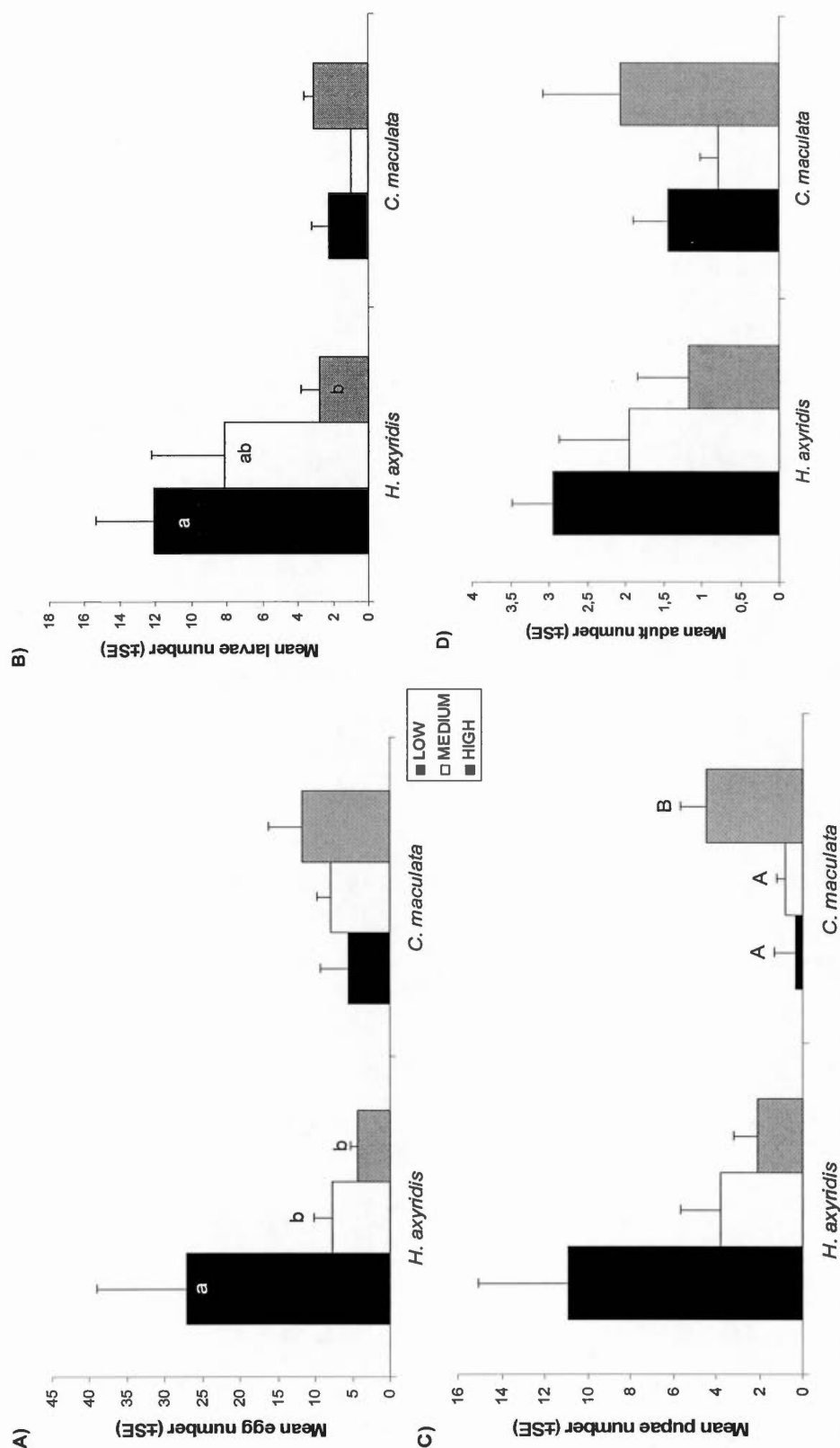


Figure IV.1. Impact of resource level on population variables of *H. axyridis* and *C. maculata* inside single species cages A) Egg number (mean \pm SE). B) Larvae number (mean \pm SE); All stages combined. C) Pupae number (mean \pm SE). D) Adult number (mean \pm SE). Note: different letters indicate significant differences among resources within a species

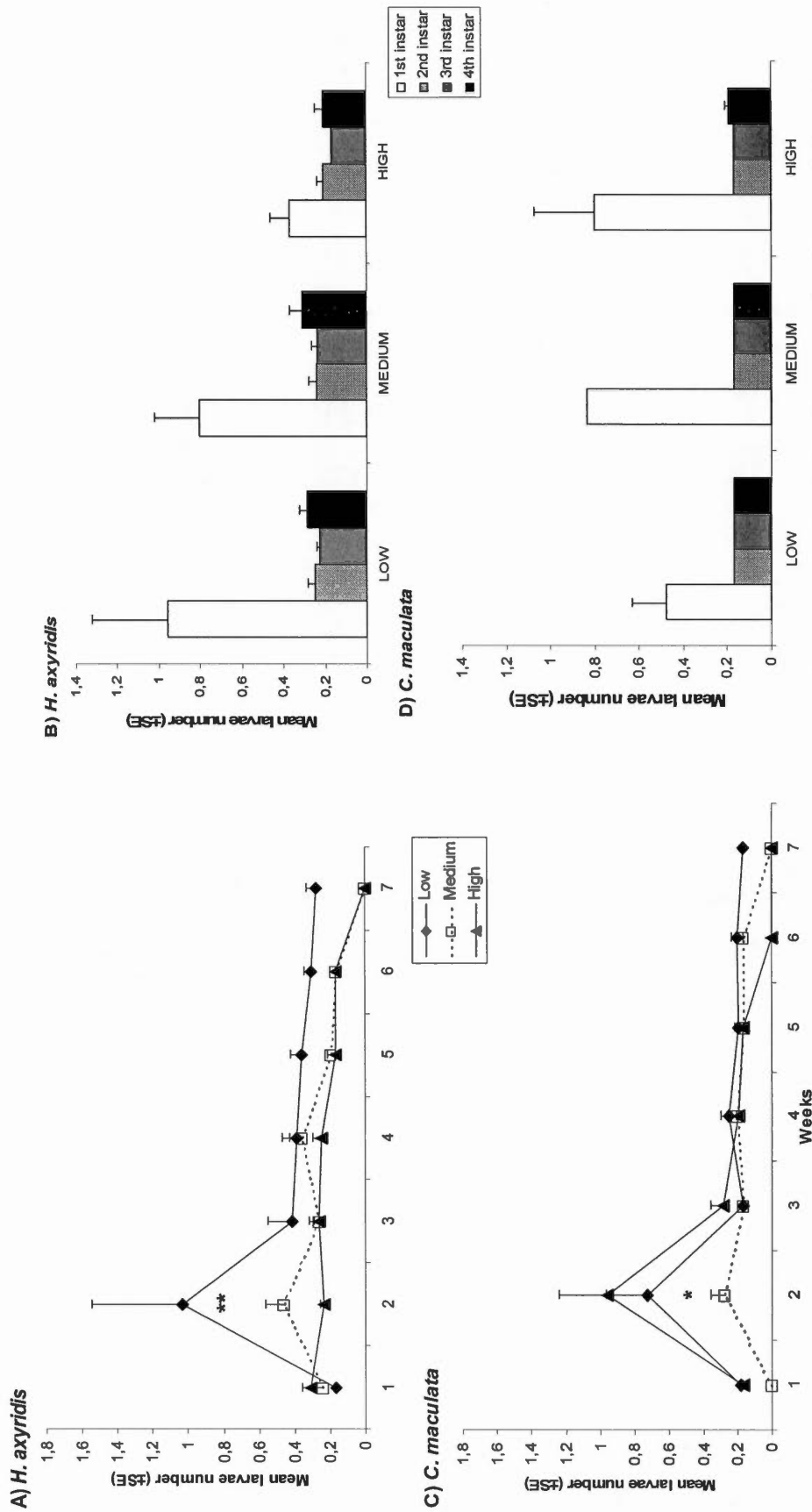


Figure IV.2. Impact of A) time and resource level on larval instar of *H. axyridis* (HA) B) of resource level on each larval instars of HA; C) time and resource level on larval instar of *C. maculata* (CM) and D) of resource level on each larval instars of CM. Note: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$

Egg spatial distribution-Alone

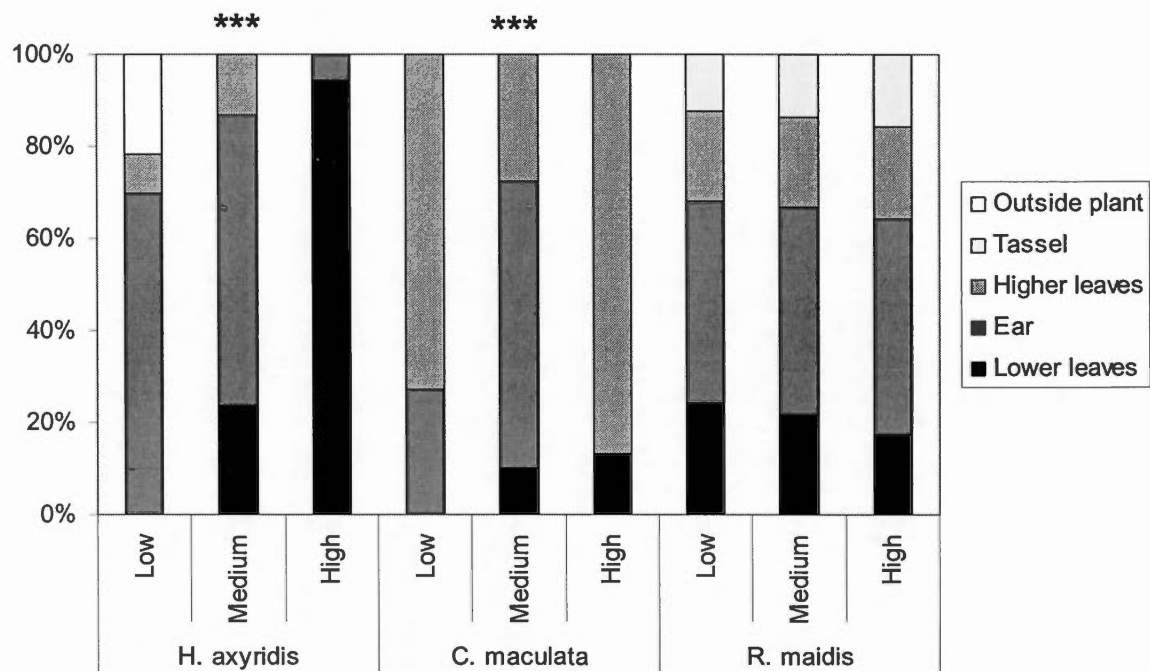


Figure IV.3. Egg spatial distribution on the corn plant of *H. axyridis* and *C. maculata* and distribution of the corn-leaf aphids *R. maidis* in three productivities. Note: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

Effects of heterospecific combination

Impact of heterospecific combinations on population variables

Larvae number of *H. axyridis* were more numerous on the mixed treatment than on the single species treatment (Table 1; 2). More pupae were observed in single species treatment in medium resource level during week 4 than in mixed treatment (Table 1; Tukey-Kramer test, $P < 0.05$). Heterospecific combination had no impact on egg or adult number of *H. axyridis* (Table 1; 2), on egg-laying time (Heterospecific combination: $F_{1,12} = 0.74$, $P = 0.41$), on developmental time (Heterospecific combination: $F_{1,12} = 0.02$, $P = 0.88$) or on survival proportion (Heterospecific combination: $F_{1,12} = 2.82$, $P = 0.12$) of *H. axyridis* (Table 2).

There was an effect of heterospecific combination on larvae and adults of *C. maculata*, which were more numerous in mixed treatment than in single species treatment (Table 1; 2). There was however no effect of heterospecific combination on egg and pupae of *C. maculata* (Table 1; 2), on egg-laying time (Heterospecific combination: $F_{1,12} = 0.24$, $P = 0.64$), developmental time (Heterospecific combination: $F_{1,10} = 0.05$, $P = 0.82$) or survival proportion (Heterospecific combination: $F_{1,12} = 0.25$, $P = 0.63$).

Impact of heterospecific combination on adult fresh biomass

No effect of heterospecific combination was observed on adult biomass of *H. axyridis* (Table 2; $F_{1,81} = 2.12$, $P = 0.15$) or of *C. maculata* (Table 2; $F_{1,46} = 0.04$, $P = 0.84$).

Effect of heterospecific combination on spatial distribution of vulnerable instars

An effect of heterospecific combination was observed on the spatial distribution of eggs of *H. axyridis* ($G_{3,720} = 164.16$, $P < 0.0001$) (Figure 4). Eggs were found in mixed treatments mostly on higher leaves at low productivity, exclusively on ears at medium productivity and on higher leaves compared to lower leaves at

high productivity in the single species treatment (Figure 4). There was more pupae outside plants in the single species treatment than in mixed treatment ($G_{4,176} = 28.17$, $P < 0.0001$).

Effect of heterospecific combination and resource level was observed on spatial distribution of eggs of *C. maculata* ($G_{2,313} = 74.39$, $P < 0.0001$) (Figure 4). Eggs in mixed treatment were not found on ear at low productivity, exclusively on ear at medium productivity and mostly on ear at high productivity compared to lower and higher leaves in single species treatment (Figure 4). Few pupae were found in the cages and no analyses were conducted on their spatial distribution.

In order to evaluate if the two species were in the same spatial niche, spatial distribution of each instar was compared between species in mixed treatments for each productivity separately. A Bonferoni correction was applied to results to avoid statistical error. Too few data were collected at the medium resource level for eggs. Egg spatial distribution differed between the two species in mixed treatment at low resource ($G_{2,252} = 22.69$, $P < 0.0001$) and at the high resource level ($G_{2,199} = 13.79$, $P = 0.001$) (Figure 4). Additional analysis were also conducted on other instars. First larval instar spatial distribution was different between the two species in mixed treatment at low resource ($G_{2,59} = 13.92$, $P = 0.001$) but not at high resource level ($G_{2,29} = 6.58$, $P = 0.04$). However, no spatial distribution differences were observed between species for 2nd instar to pupae ($P > 0.05$), demonstrating that spatial distribution of the two species overlapped widely during the course of the experiment.

Cannibalism and intraguild predation

A total of 26 events of cannibalism were noted in the different productivities and treatments during the 7 weeks of observations, 5 by *C. maculata* and 21 by *H. axyridis*. All stages of development were involved in the cannibalism. A mean cannibalism number of 1.0 ± 0.0 and a relative cannibalism (number of CNB events/larvae number present in the cages) of $26.3 \pm 7.4\%$ were observed only in the

cages alone by *C. maculata*, that were not significantly different between resource level ($\chi^2 = 0.80$; $df = 2$; $P = 0.87$). Relative cannibalism of *C. maculata* ranged between 7 and 33% and were observed in the three productivities. A mean cannibalism number of 1.4 ± 0.16 and a relative cannibalism of 14.9 ± 3.2 were observed in all cages (single species and mixed) for *H. axyridis*, that was not significantly different between resource level ($\chi^2 = 0.45$; $df = 2$; $P = 0.58$). Relative cannibalism of *H. axyridis* ranged between 5 and 33% and was equally present in all productivities or treatment.

We observed 3 intraguild predation events of *H. axyridis* on *C. maculata*, with two events at low resource level and one at high resource level. Total duration of the experiment was 70560 minutes, of which we observed only 0.3%. If we suppose IGP events at a constant rate throughout the experiment, we could estimate an incidence of 1.11 IGP event/cage by *H. axyridis* on *C. maculata*.

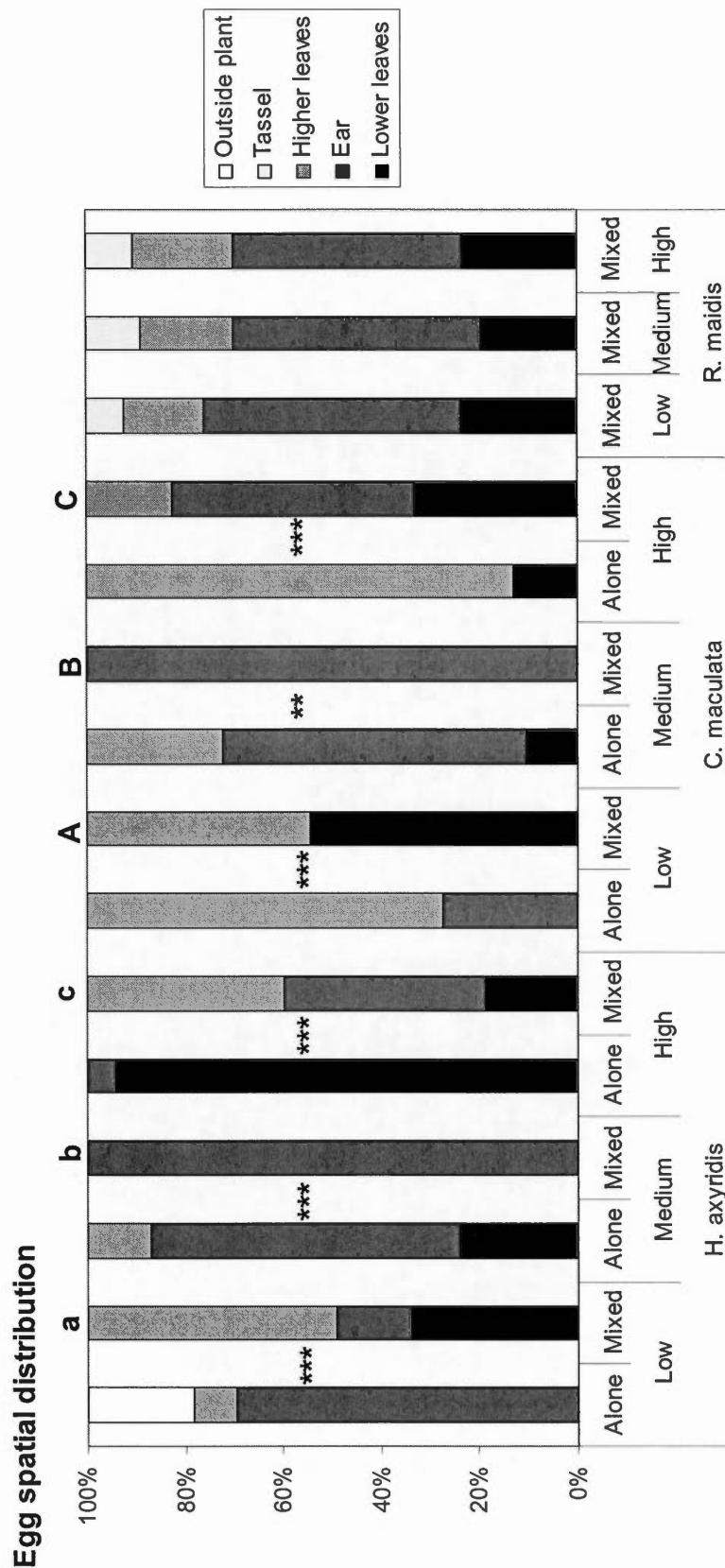


Figure IV.4. Effect of heterospecific combination on egg spatial distribution of *H. axyridis* and *C. maculata* and spatial distribution of *R. maidis* in mixed treatment in three productivities. Note: * indicate significant differences among single species and mixed treatment within species. Correction of Bonferroni are applied to results. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. Letters indicate significant differences between productivities for each species in mixed treatment.

IV.5 DISCUSSION

Neither productivity nor the presence of a competitor affected the invasive *H. axyridis* as expected. Opposite effect of resource productivity was observed for egg and larvae number of the invasive ladybeetle, which were more numerous in low resource level than other productivity. Furthermore, coexistence between *H. axyridis* and *C. maculata* was observed at all resource productivities, while models indicated coexistence at intermediate levels. Oviposition strategy of the females, incidence of cannibalism and spatial refugia could explain these results.

Effects of resource productivity on population variables of the invasive species

For an individual that is invading a new environment, the quantity of resource could be a determinant of its own survival and further survival of its young (Marco *et al.* 2002; Tilman 1999). While there was different resource productivity in our cages, we did not found different number of adults of the invasive *H. axyridis* after a two months experiment. We expected a difference as resource intake will affect growth and adult biomass (Dixon and Hemptinne 2001). Hoogendoorn and Heimpel (2004) introduced 1st larval instar of *H. axyridis* and *C. maculata* in field cages of corn plants at low (50 *R. maidis*) and high resource level (200 *R. maidis*). Number of recovered larvae of *H. axyridis* was higher in high prey treatment after one week than at lower resource level. Our results demonstrated the opposite effect after one week of experiment. More larvae were observed at lower resource than at medium or high levels (Figure 1B; Figure 2A), that is consistent with higher egg number found in these cages. However, this difference disappears the next week and pupae and adult number were the same in all productivities at the end of experiment. Adult biomass was also the same, indicating that individuals could adjust their energy conversion of food into growth (Hodek and Honěk 1996). Experiments demonstrated that 1st larval instar are very vulnerable to starvation (Dixon 1959), exploitative competition or intra or interspecific interactions (Cottrell and Yeargan 1998; Cottrell 2004; Michaud

2003; Yasuda *et al.* 2001). In our experiment, greater mortality of larvae was observed in all treatments after the second week (Figure 2A, B) and only half of the 1st instars developed to 2nd instars in all resource levels and for the two species. Osawa (1993) showed that the mortality of larva was a key factor for the population of *H. axyridis*. Our results indicate that population pressure, by starvation or competition, is mainly on juveniles. Choice of oviposition site, far from predators but near aphids colony, and number of eggs to be laid could thus be crucial for females of the invasive species (Osawa 2003).

Reproductive strategies could explain success of a species in a new environment. Ladybird predators prefer to lay eggs when aphid colonies are in early phase of development, with few young aphids and no accumulation of honeydew (Agarwala *et al.* 2001; Agarwala and Batthacharya 1995; Dixon 2000; Kindlmann and Dixon 1993). If eggs are laid later, the aphid colony might disperse and disappear before the ladybird larvae complete their development (Fréchette *et al.* 2003). Study of Osawa (2000) suggested that *H. axyridis* adults can detect the quantity and quality of aphids in a field. In our experiment, more eggs were laid by females at low resource level, suggesting that females *H. axyridis* choose young aphid colonies with low number of individuals, which could ensure better survival of young. No such results were observed for the indigenous species, which did not lay different egg number in different habitats.

Oviposition site selection might also reflect a trade-off between laying eggs near an aphid colony, where intraguild predation and cannibalism are likely to be intense, but foraging of neonate larvae more successful, and laying eggs at a distance from an aphid colony where interference would be lower but neonate larvae more susceptible to starvation (Lucas and Brodeur 1999; Osawa 2003). Presence of aphids (Evans and Dixon 1986), conspecifics (Agarwala and Dixon 1992; Agarwala and Batthacharya 1995; Agarwala *et al.* 2003; Fréchette *et al.* 2003; Osawa 2003) or heterospecifics (Burgio *et al.* 2002; Mills 1982; Soares and Serpa 2007) will

theoretically affect oviposition site selection of ladybeetles (Burgio *et al.* 2002; Mills 1982; Osawa 1989; 1993). In the experiment of Agarwala *et al.* (2003), *H. axyridis* avoided to oviposit on plants with presence of conspecifics feces, but not in presence of heterospecific *Propylea japonica* L. Our results showed that *H. axyridis* oviposit mostly outside plants in single species treatment, where only conspecifics were present. Osawa (2003) suggested that *H. axyridis* oviposition strategy is to control non-sibling cannibalism, by determining safe distance from aphid colony and cluster size. Laying egg far from young aphid colony could reduce non-sibling cannibalism, even if mortality by sibling cannibalism will be high. Cannibalism is an important mortality factor in natural population of several species of ladybird beetles (Osawa 1989; 1993; Hironori and Katsuhiko 1997) and could be among the most important mortality factors for juvenile coccinellids (Dixon 2000; Schellhorn and Andow 1999; Wright and Laing 1982). In a natural population of *H. axyridis*, cannibalism occurred in more than 90% of all clusters (Osawa 1989), and approximately 30% of eggs were killed by sibling cannibalism (Osawa 1993). In our experiment, *H. axyridis* cannibalism ranged from 8% to 33%. Osawa (1993; 2000) supposed that the density-dependent mortality of larval stages and egg cannibalism made *H. axyridis* population rather persistent and stable under fluctuating resource conditions. *Harmonia axyridis* is more voracious than *C. maculata* and needs more aphids to grow, thus, extinction of the invasive ladybeetle in low resource level was expected until the end of experiment. However, we suggest that oviposition strategy and cannibalism at low resource level had benefited individuals by reducing mortality by starvation and ensuring growth and survival of the same number of individuals than in richer habitats.

Effect of resource productivity on interactions and coexistence

Invasive success of a species could be reduced by competition with indigenous species (Costanzo *et al.* 2005; Levine *et al.* 2003). The presence of a competitor affected larvae number of the two ladybeetles and adult number of *C.*

maculata. However, there was more individuals in the mixed cages than in single species cages. Our experimental design, six introduced females in single species treatment versus three females of each species in the mixed treatment did not allow us to measure directly influence of intraguild predation and productivity on the coexistence of the two species. We can distinguish however the pressure of interspecific compared to intraspecific competition as conspecific females were half number in mixed cages than in single species cages. We expected thus some negative impacts in mixed cage if interspecific interactions were stronger than intraspecific interactions. It was not the case. More individuals were found in mixed cages than in single species cages, indicating that intraspecific interactions are influencing more negatively the ladybeetles individuals than interspecific interactions. Even if intraguild predation in the field is not easy to detect, we observed nonetheless some IGP events of *H. axyridis* on *C. maculata*. Duration of observation in each cage was very short and we suspected other IGP events. However, more cannibalism events were observed for the two species during all experiments. Furthermore, cannibalism events were observed only on single species treatment for the indigenous species and we found more adults of *C. maculata* in mixed treatment at the end of experiment than in single species cages. Another point that could indicate stronger pressure by intraspecific competition is spatial distribution of vulnerable instars. In single species treatment, eggs and pupae of *H. axyridis* were found outside plants, while no such pattern was observed in mixed cages. According to theory, (Mylius et al. 2001), presence of *C. maculata* was expected at low productivity, while *H. axyridis* was supposed to exclude *C. maculata* at high productivity, by achieving higher population number and stronger predation pressure. This pattern was not observed at all resource levels. We could thus not infirm this theory in our experiment. Schellhorn and Andow (1999) suggested that coexistence is possible between two interacting species in an intraguild predation scheme if the species interfere with itself at least as much as it interferes with the other. Invasive success of *H. axyridis* was not reduced in presence of a competitor. Furthermore, we suggest that intraspecific competition,

particularly cannibalism of *H. axyridis*, can reduce predation pressure on the indigenous *C. maculata* and may explain the coexistence of the two species at different resource productivity in our experiment.

Following theory, functionally similar species that use same spatial and trophic niches will compete intensely and one species will exclude the other (Bando 2006; Dudgeon *et al.* 1999). We demonstrated that spatial distribution of the two species overlap widely in mixed cages for less vulnerable instars. These results contradict observations of Musser and Shelton (2003), that found that *H. axyridis* were found on top part of the plant and *C. maculata* on the lower part of the plant. However, Lucas *et al.* (2002) demonstrated no niche differentiation between adults of *H. axyridis*, *C. septempunctata*, and *C. maculata* foraging on apple saplings in laboratory. Extinction of the indigenous ladybeetle in our cages was expected. However, eggs and 1st instar larvae of the two species were not found at the same place on plants when in presence of each other. At low resource level, *C. maculata* avoid to oviposit on ear of corn plants, where aphids are in higher number and where eggs of *H. axyridis* were found. Egg-laying time and developmental time were also similar between the ladybeetles (Table 2), indicating that they use similar temporal niche. The degree of habitat and microhabitat overlap among the species and the timing of arrival and larval development of individual species in a given habitat may also influence interspecific interactions (e.g. Coderre *et al.* 1987; Musser and Shelton 2003). For example, Evans (2004) demonstrated that the invasive *C. septempunctata* persisted in higher number in fields with lower number of aphids than indigenous species, that were just passing through these habitats in search of prey. The establishment of this invasive species has thus limited significantly the potential for aphids to reach high number in these habitats, thereby reducing the numerical response for native species. *Harmonia axyridis* often tends to arrive and oviposit later in habitats than other ladybirds species (Musser and Shelton 2003; Nault and Kennedy 2003). We observed this pattern in corn field of Quebec (Labrie *et al.*

unpublished data). In previous experiment, we also demonstrated that *H. axyridis* eggs and young instars were vulnerable to intraguild predation by *C. maculata* or *P. quatuordecimpunctata* (Labrie *et al.* Chapter II). Other species may derive protection by co-occurring as older larvae with younger larvae of *H. axyridis* (e.g. Sato and Dixon 2004). These situations could lead to alternative stable states, where coexistence will be possible (Chase 1999). Our experiment did not demonstrate however differences in egg-laying time, and we cannot evaluate if the presence of *H. axyridis* before *C. maculata* could lead to reduction of the indigenous species. Furthermore, we did not quantify numerical aggregative responses of ladybeetles or total fecundity of females in presence of conspecifics or heterospecifics, that could mitigate the results. Further experiments are needed to evaluate these situations.

Conclusion

Phenotypic plasticity has often been cited as a life-history trait needed for colonization of new areas because colonists must be able to cope with a range of new environmental conditions (see Sakai *et al.* 2001). Our results suggest that *H. axyridis* present high environmental tolerance to different resource quantity and phenotypic plasticity with oviposition decisions of the females, presence of sibling cannibalism and spatial refugia for vulnerable instars. Changes in behavior, physiology, morphology, growth, life history, and demography express plastic responses of a species, that can be expressed either within the lifespan of a single individual or across generations (Miner *et al.* 2005; Sakai *et al.* 2001). Many studies demonstrate that plasticity can promote stability, species coexistence or both (Vos *et al.* 2004; Verschoor *et al.* 2004; Persson and De Roos 2003; Krivan and Diehl 2005; Hui *et al.* 2004). Changes in egg number and spatial niche of *H. axyridis* with resource and competitor presence could indicate that *H. axyridis* recognize biotic factors that could affect its survival. Furthermore, when a species is more plastic in a tri-trophic system, predicted extinctions could not arise because the plasticity of the species induce a stabilization of the system (Miner *et al.* 2005). Plasticity of *H. axyridis* in switching

prey preference or spatial niche could thus explain why there was no extinction of *C. maculata* at high resource, as predicted by theoretical models (Diehl and Feissel 2001; Mylius *et al.* 2001). Some negative effects of invasion of *H. axyridis* could however be possible with more specialized species. It was suggested that the invasive *C. septempunctata*, more aphidophagous than *H. axyridis* or *C. maculata*, could be displaced by *H. axyridis* (Brown and Miller 1998; Colunga-Garcia and Gage 1998). More studies are needed in fields to evaluate the impact of the invasive *H. axyridis* on other ladybeetles species at different resource productivity. Plasticity of *H. axyridis* along with life-history traits (Labrie *et al.* 2006), competitive abilities (Labrie *et al.* Chapter II) and use of houses as overwintering sites (Labrie *et al.* in press), may explain great invasive success of the multicoloured Asian ladybeetle in many part of the world.

IV.6 ACKNOWLEDGEMENTS

We thank Annie-Ève Gagnon-Thibodeau, Raphaël Dubé, Isabelle Desjardins and Janick Durocher for their technical assistance. Special thanks to Samuel Pinna and William Vickery for revision of an earlier draft of the document. This research was supported by an NSERC scholarship granted to G. Labrie, NSERC grant to D. Coderre and E. Lucas.

IV.7 REFERENCES

- Agarwala, B. K. and Dixon, A.F.G. (1992) Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecological Entomology* **17**, 303-309.
- Agarwala, B. K. and Bhattacharya, S. (1995) Adaptive features of the predatory ladybird beetles in uncertain and competitive habitats. *Current Science* **69**, 587-591.
- Agarwala, B. K., Bardhanroy, P., Yasuda, H. and Takizawa, T. (2001) Prey consumption and oviposition of the aphidophagous predator *Menochilus sexmaculatus* (Coleoptera : Coccinellidae) in relation to prey density and adult size. *Environmental Entomology* **30**, 1182-1187.
- Agarwala, B. K., Yasuda, H. and Kajita, Y. (2003) Effect of conspecific and heterospecific feces on foraging and oviposition of two predatory ladybirds: role of fecal cues in predator avoidance. *Journal of Chemical Ecology* **29**, 357-376.
- Balciunas, D. and Lawler, S.P. (1995) Effects of basal resources, predation, and alternative prey in microcosm food chains. *Ecology* **76**, 1327-1336.
- Bando, K. J. (2006) The roles of competition and disturbance in a marine invasion. *Biological Invasions*, **8**, 755-763.
- Bohannan, B. J. M. and Lenski, R. E. (1999) Effect of prey heterogeneity on the response of a model food chain to resource enrichment. *American Naturalist* **153**, 73-82.
- Brown, M. W. (2003) Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl* **48**, 141-153.
- Brown, M. W. and Miller, S. S. (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News* **109**, 143-151.

- Burgio, G., Santi, F. and Maini, S. (2002) On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). *Biological Control* **24**, 110-116.
- Burke, M. J. W., and Grime, J. P. (1996) An experimental study of plant community invasibility. *Ecology* **77**, 776– 790.
- Chase, J. M. (1999) Food web effects of prey size refugia: variable interactions and alternative stable equilibria. *American Naturalist* **154**, 559-570.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematic* **31**, 343-366.
- Coderre, D., Lucas, E. and Gagne, I. (1995) The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) in Canada. *Canadian Entomologist* **127**, 609-611.
- Coderre, D., Provencher, L. and Tourneur, J.-C. (1987) Oviposition and niche partitioning in aphidophagous insects on maize. *Canadian Entomologist* **119**, 195-203.
- Colunga-Garcia, M. and Gage, S. H. (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology* **27**, 1574-1580.
- Costanzo, K.S., Desavaraju, B. and Juliano, S.A. (2005) Condition-specific competition in container mosquitoes: the role of noncompeting life-history stages. *Ecology* **86**, 3289-3295.
- Cottrell, T. E. and Yeargan, K. V. (1998) Intraguild predation between an introduced lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Journal of Kansas Entomological Society* **71**, 159-163.

- Cottrell, T. E. (2004) Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biological Control* **31**, 362-371.
- Diehl, S. and Feissel, M. (2000) Effects of enrichment on three-level food chains with omnivory. *American Naturalist* **155**, 200-218.
- Diehl, S. and Feissel, M. (2001) Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. *Ecology* **82**, 2977-2983.
- Dixon A.F.G. (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia bipunctata* (L.) *Journal of Animal Ecology* **28**, 259-281.
- Dixon, A. F. G. (2000). Insect predator-prey dynamics: ladybird beetles and biological control. Cambridge, Cambridge University Press.
- Dixon, A.F.G. and Hemptinne, J.L. (2001) Body size distribution in predatory ladybird beetles reflects that of their prey. *Ecology* **82**, 1847-1856.
- Drake, J.A., Mooney, H.A., diCasti, F., Groves, R.H., Kruger, F.J., Rejmanek, M. and Williamson, M. (1989) Biological invasions: a global perspective. SCOPE, John Wiley and Sons Ltd.
- Dudgeon, S.R., Steneck, R.S., Davison, I.R. and Vadas, R.L. (1999) Coexistence of similar species in a space-limited intertidal zone. *Ecological Monographs* **69**, 331-352.
- Evans, E.W. (2004) Habitat displacement of North American ladybirds by an introduced species. *Ecology* **85**, 637-647.
- Evans, E.W. and Dixon, A.F.G. (1986) Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. *Journal of Animal Ecology* **55**, 1027-1034.
- Firlej, A., Boivin, G., Lucas, E. and Coderre, D. (2005) First report of *Harmonia*

- axyridis* Pallas being attacked by *Dinocampus coccinellae* Schrank in Canada. *Biological Invasions* **7**, 553-556.
- Fréchette, B., Alauzet, C. and Hemptinne, J.-L. (2003). Oviposition behaviour of the two-spot ladybird beetle *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) on plants with conspecific larval tracks. Pp. 73 *In* Soares, A. O. Ventura, M. A., Garcia, V. and Hemptinne J.-L. (eds) *Proceeding of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidiphagous Insects.*, Azores, Arquipélago-Life and Marine Science. Supplement 5: x + 112 pp.
- Fréchette, B., Dixon, A. F. G., Alauzet, C. and Hemptinne, J.-L. (2004) Age and experience influence patch assessment for oviposition by an insect predator. *Ecological Entomology* **29**, 578-583.
- Hanski, I. 1989. Does it help to have more of the same? *Trends in Ecology and Evolution* **4**: 113-114.
- Hironori, Y. and Katsuhiko, S. (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* **42**, 153-163.
- Hodek, I. and Honěk, A. (1996) *Ecology of Coccinellidae*. Kluwer Academic Publishers, Netherlands, 464 p.
- Holt, R. D. and Polis, G. A. (1997) A theoretical framework for intraguild predation. *American Naturalist* **149**, 745-764.
- Hoogendoorn, M. and Heimpel, G. E. (2004) Competitive interactions between an exotic and a native ladybeetle: a field cage study. *Entomologia Experimentalis et Applicata* **111**, 19-28.
- Hui, C., Li, Z. and Yue, D.-X. (2004) Metapopulation dynamics and distribution, and environmental heterogeneity induced by niche construction. *Ecological*

Modelling **177**, 107-118.

- Kiesecker, J.M., Blaustein, A.R. and Miller, C.L. (2001) Potential mechanisms underlying the displacement of red-legged frogs by introduced bullfrogs. *Ecology* **82**, 1964-1970.
- Kindlmann, P. and Dixon, A. F. G. (1993) Optimal foraging in ladybird beetles (Coleoptera, Coccinellidae) and its consequences for their use in biological control. *European Journal of Entomology* **90**, 443-450.
- Kotler, B.P. and Brown, J.S. (1988) Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* **19**, 281-307
- Krivan, V. and Diehl, S. (2005) Adaptive omnivory and species coexistence in tri-trophic food webs. *Theoretical Population Biology* **67**, 85-99.
- Labrie, Coderre, D. and Lucas, E. (2007) Overwintering strategy of the multicolored Asian ladybeetle (Coleoptera: Coccinellidae): a cold-free space as a factor of invasive success. *Annals of the Entomological Society of America*, **in press**.
- Labrie, G., Lucas, E. and Coderre, D. (2006) Can developmental and behavioral characteristics of the multicolored Asian lady beetle *Harmonia axyridis* explain its invasive success? *Biological Invasions* **8**, 743-754.
- Lambrinos, J.G. (2006) Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass. *Oecologia* **147**, 327-334.
- Levine, J. M. and D'Antonio, C. M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**, 15-26.
- Levine, J.M. Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. and Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B* **270**, 775-781.
- Lucas, E. (2005) Intraguild predation among aphidophagous predators. *European Journal of Entomology* **102**, 351-364.

- Lucas, E., Coderre, D. and Brodeur, J. (1998) Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* **79**, 1084-1092.
- Lucas, E. and Brodeur, J. (1999) Oviposition site selection by the predatory midge *Aphidoletes aphidimyza* (Diptera : Cecidomyiidae). *Environmental Entomology* **28**, 622-627.
- Lucas, E., Gagné, I. and Coderre, D. (2002) Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology* **99**, 457-463.
- Lucas, E., Labrie, G., Vincent, C. and Kovach, J. (in press) The multicoloured Asian lady beetle *Harmonia axyridis* – beneficial or nuisance organism? In Vincent, C., Goettel, M. And Lazarovitz, G. (eds.) Case studies in biological control : a global perspective. CABI Publishing, UK.
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. and Bazzaz, F. A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**, 689-710.
- Marco, D. E., Paez, S. A. and Cannas, S. A. (2002) Species invasiveness in biological invasions: a modelling approach. *Biological Invasions* **4**, 193-205.
- McClure, M. S. (1987) Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* bean and godwin (Homoptera: Margarodidae) in the United States. *Environmental Entomology* **16**, 224-230.
- Michaud, J. P. (2003) A comparative study of larval cannibalism in three species of ladybird. *Ecological Entomology* **28**, 92-101.
- Mills, N. J. (1982) Voracity, cannibalism and coccinellid predation. *Journal of Applied Biology* **101**, 144-148.

- Miner, B. G., Sultan, S. E., Morgan, S. G., Padilla, D. K. and Relyea, R. A. (2005) Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution* **20**, 685-692.
- Morin, P. (1999) Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology* **80**, 752-760.
- Müller, C. B. and Brodeur, J. (2002) Intraguild predation in biological control and conservation biology. *Biological Control* **25**, 216-223.
- Musser, F. R. and Shelton, A. M. (2003) Factors altering the temporal and within-plant distribution of coccinellids in corn and their impact on potential intraguild predation. *Environmental Entomology* **32**, 575-583.
- Mylus, S. D., Klumpers, K., de Roos, A. M. and Persson, L. (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist* **158**, 259-276.
- Nault, B. A. and Kennedy, G. G. (2003) Establishment of multicolored Asian lady beetle in Eastern North Carolina: seasonal abundance and crop exploitation within an agricultural landscape. *BioControl* **48**, 363-378.
- Obrycki, J. J., Giles, K. L. and Ormord, A. M. (1998) Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia* **117**, 279-285.
- Osawa, N. (1989) Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Researches in Population Ecology* **31**, 153-160.
- Osawa, N. (1993) population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life table and key factor analysis. *Researches in Population Ecology* **35**, 335-348.
- Osawa, N. (2000) Population field studies on the aphidophagous ladybird beetle

- Harmonia axyridis* (Coleoptera : Coccinellidae): resource tracking and population characteristics. *Population Ecology* **42**, 115-127.
- Osawa, N. (2003) The influence of female oviposition strategy on sibling cannibalism in the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology* **100**, 43-48.
- Park, Y.-L. and Obrycki, J. J. (2004) Spatio-temporal distribution of corn leaf Aphids (Homoptera: Aphididae) and ladybeetles (Coleoptera: Coccinellidae) in Iowa cornfields. *Biological Control* **31**, 210-217.
- Persson, L. and De Roos, A. M. (2003) Adaptive habitat use in size-structured populations: linking individual behavior to population processes. *Ecology* **84**, 1129-1139.
- Pervez, A. and Omkar (2006) Ecology and biological control application of multicoloured Asian ladybird, *Harmonia axyridis*: A review. *Biocontrol Science and Technology* **16**, 111-128.
- Pimentel, D., Zuniga, R. And Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**, 273-288.
- Polis, G. A., Myers, C. A. and Holt, R. D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**, 297-330.
- Ricciardi, A. (2004) Assessing species invasions as a cause of extinction. *Trends in Ecology and Evolution* **19**, 619.
- Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N. and Weller, S. G. (2001) The population biology of invasive species. *Annual Review of Ecology and*

Systematics **32**, 305-332.

- Sato, S. and Dixon, A. F. G. (2004) Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. *Agricultural and Forest Entomology* **6**, 21-24.
- Schellhorn, N. A. and Andow, D. A. (1999) Cannibalism and interspecific predation: Role of oviposition behavior. *Ecological Applications* **9**, 418-428.
- Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* **17**, 170-176.
- Simberloff, D., Parker, I.M. and Windle, P.N. (2005) Introduced species policy, management, and future research needs. *Frontiers of Ecology and Environment* **3**, 12-20.
- Snyder, W. E., Clevenger, G. M. and Eigenbrode, S. D. (2004) Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia* **140**, 559-565.
- Soares, A. O. and Serpa, A. (2007) Interference competition between ladybird beetle adults (Coleoptera: Coccinellidae): effects on growth and reproductive capacity. *Population Ecology*, **49**, 37-43.
- Sokal, R. R. and Rohlf, F. J. (1995). Biometry: the principles and practice of statistics in biological research. 3rd Edition. San Francisco., W. H. Freeman.
- Spiller, D.A. and Schoener, T.W. (1994) Effects of top and intermediate predators in a terrestrial food web. *Ecology* **75**, 182-196.
- Tedders, W. L. and Schaefer, P. W. (1994) Release and establishment of *Harmonia axyridis* (Coleoptera, Coccinellidae) in the southeastern United-States. *Entomological News* **105**, 228-243.
- Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455-1474.

- Verschoor, A. M., Vos, M. and van der Stap, I. (2004) Inducible defences prevent strong population fluctuations in bi- and tritrophic food chains. *Ecology Letters* **7**, 1143-1148.
- Von Holle, B. and Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* **86**, 3212-3218.
- Vos, M., Kooi, B. W., DeAngelis, D. L. and Mooij, W. M. (2004) Inducible defences and the paradox of enrichment. *Oikos* **105**, 471-480.
- With, K. A., Pavuk, D. M., Worchuck, J. L., Oates, R. K. and Fisher, J. L. (2002) Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications* **12**, 52-65.
- Wright, E. J. and Laing, J. E. (1982) Stage-specific mortality of *Coleomegilla maculata lengi* Timberlake on corn in southern Ontario. *Environmental Entomology* **11**, 32-37.
- Yasuda, H. and Ohnuma, N. (1999) Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia Experimentalis et Applicata* **93**, 63-67.
- Yasuda, H., Kikuchi, T., Kindlmann, P. and Sato, S. (2001) Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior* **14**, 373-384.
- Yasuda, H., Evans, E. W., Kajita, Y., Urakawa, K. and Takizawa, T. (2004) Asymmetric larval interactions between introduced and indigenous ladybirds in North America. *Oecologia* **141**, 722-731.

CONCLUSION GÉNÉRALE

Une invasion réussie par une espèce végétale ou animale peut se résumer à 3 composantes et leurs interactions : l'espèce, la communauté et l'environnement (Shea et Chesson 2002; Shea *et al.* 2005). L'espèce envahissante doit posséder les caractéristiques biologiques qui lui permettront de s'installer et de se reproduire dans le nouveau milieu. Elle devra être en mesure de s'y insérer, d'interagir efficacement avec la communauté d'espèces déjà en place, soit par des interactions directes ou indirectes. Elle devra faire face à diverses conditions environnementales, soit abiotiques comme la température, l'humidité, le pH etc. ou biotiques, comme la quantité de ressources, l'hétérogénéité et la complexité de l'environnement etc. La coccinelle asiatique est exemplaire de cette équation. A l'heure actuelle, son invasion est pratiquement planétaire! Les introductions répétées aux États-Unis de 1978 à 1982 (Teddies et Schaefer 1994) ont porté fruit. Après la première mention en 1988 en Louisiane de quelques individus de la coccinelle asiatique dans des vergers de pacaniers, elle est arrivée au Québec en 1994 et depuis ce temps, elle ne cesse de s'étendre dans le reste du Canada et des États-Unis (Alyokhin and Sewell 2004; Brown 2003; Mignault *et al.* 2006; Musser et Shelton 2003; Turnock *et al.* 2003). Il y a eu récemment les premières mentions de la coccinelle asiatique en Amérique du Sud : en Argentine en 2001 (Saini 2004) et au Brésil en 2002 (De Almeida et da Silva 2002). Elle a été retrouvée en Belgique en 2002 (Adriaens *et al.* 2003; San Martin *et al.* 2005), en Allemagne, en Grèce et récemment en Grande-Bretagne (Majerus *et al.* 2006). Elle est devenue dominante dans de nombreux écosystèmes au Québec (voir Lucas *et al.* Annexe A), causant de nombreux inconvénients, autant pour les autres espèces de prédateurs aphidiphages qu'aux humains (voir Lucas *et al.* Annexe B). Notre travail a permis d'identifier plusieurs ingrédients de la recette du succès d'invasion de la coccinelle asiatique.

Le premier ingrédient de la recette est la survie hivernale de la coccinelle asiatique dans nos régions. Les conditions hivernales rencontrées au Québec

semblaient un bon frein à l'invasion de cette espèce, du fait que les populations introduites provenaient d'une région où elles ne toléraient pas des températures sous -15°C (Watanabe 2002). Nos résultats ont ainsi démontré que cette espèce ne survivait pas à l'extérieur sous nos hivers rigoureux (Labrie *et al.* sous presse). Toutefois, le comportement d'hiberner dans les habitations lui permet de survivre à l'hiver, et probablement à un meilleur taux que les coccinelles indigènes, qui meurent de froid, noyées, parasitées ou infectées par des champignons. Nous avons donc suggéré que la coccinelle asiatique bénéficiait d'un espace libre de *froid* (*cold-free space*) qui lui permettrait de réussir son invasion. Cette hibernation dans les habitations est donc une caractéristique cruciale pour l'invasion de la coccinelle. Sans cette utilisation des habitations, la coccinelle asiatique n'aurait probablement pas été capable d'envahir le Québec et les régions plus nordiques de la planète. La question qui se pose face à cette situation est jusqu'où la coccinelle asiatique survit-elle dans le nord du Québec? S'arrête-t-elle aux dernières habitations humaines? Nous pouvons formuler l'hypothèse, qui restera à vérifier, que la présence des coccinelles plus au nord s'arrête dès que les habitations sont absentes.

Le deuxième ingrédient de la recette est lié aux stades de développement de la coccinelle asiatique. Nous avons pu découvrir que la coccinelle se développe plus rapidement vers des stades moins vulnérables, avec une meilleure conversion d'énergie au 2^{ème} stade larvaire (Labrie *et al.* 2006). Nous avons pu démontrer au Chapitre 2 qu'elle était très vulnérable à la prédation intragilde à ces stades; un développement plus rapide vers les stades plus gros et moins vulnérables à la prédation est donc un atout pour une espèce envahissante. Nous avons aussi observé l'apparition d'un 5^{ème} stade larvaire dans un milieu optimal, plus vorace, plus gros, avec un potentiel reproducteur plus grand et une efficacité de prédation plus élevée (Labrie *et al.* 2006). Si ce stade surnuméraire peut être induit, cette caractéristique serait donc un atout majeur pour cette espèce envahissante (Labrie *et al.* 2006). Bien que nous ayons pu observer au champ des larves de la coccinelle asiatique très

semblables aux larves de 5^{ème} stade retrouvées au laboratoire (Labrie, observation personnelle), il reste encore des études à effectuer afin de mieux comprendre ce phénomène.

Le troisième ingrédient de la recette est la vulnérabilité moindre de la coccinelle asiatique à la prédation intragilde au 4^{ème} stade larvaire ainsi qu'au stade pupal (Chapitre 2). Aucun stade de la coccinelle maculée et de la coccinelle à 14 points n'ont consommé ces deux stades dans les Petri lors de nos expériences au laboratoire. Le quatrième stade larvaire de la coccinelle asiatique est très agressif (Yasuda *et al.* 2001; 2004), ce qui peut expliquer l'absence de prédation intragilde sur ce stade. Toutefois, le stade pupal est un stade habituellement très vulnérable à la prédation (Lucas *et al.* 2000; Majerus 1994). Sa faible vulnérabilité à ces stades peut être un atout pour l'invasion de cette espèce.

Le dernier ingrédient de la recette, qui vient amalgamer le tout, est la plasticité de la coccinelle asiatique. Dans le dernier chapitre, nous avons démontré que la coccinelle asiatique était peu influencée par la quantité de ressources du milieu car le nombre d'adultes par femelles introduites était le même à tous les niveaux de productivité du milieu à la fin de l'expérience. La stratégie d'oviposition des femelles, le cannibalisme et la distribution spatiale des stades plus vulnérables peuvent expliquer ces résultats. Cette espèce semble donc s'adapter aux différentes conditions abiotiques, telles le climat, biotiques, comme la quantité de ressource ou la présence de compétiteurs. Sa capacité à envahir différentes régions du monde démontre bien cette plasticité. Grill *et al.* (1997) ont démontré que la variation génétique de la coccinelle asiatique pouvait lui permettre des changements adaptatifs dans les taux de développement et dans la taille. Le 5^{ème} stade larvaire pourrait être un de ces changements adaptatifs liés à sa grande plasticité. La plasticité de la coccinelle asiatique est donc une caractéristique qui lui permet d'envahir de nouveaux habitats avec succès.

D'autres ingrédients à la recette du succès d'invasion de la coccinelle asiatique ont déjà été démontrés par d'autres études. Ainsi, la coccinelle asiatique peut se reproduire beaucoup plus que les autres espèces de coccinelles, pouvant déposer jusqu'à un maximum de 3800 œufs dans la vie d'une seule femelle en laboratoire (Hodek 1973; Soares *et al.* 2001). Une grande fécondité et fertilité est une des caractéristiques qui peut permettre d'envahir avec succès un nouvel environnement. De plus, elle semble libre d'ennemis naturels. Ainsi, Firlej *et al.* (2005), ont pu montrer que cette coccinelle est peu attaquée par le parasitoïde *D. coccinellae* au Québec, et que les larves de parasitoïdes ne peuvent se développer à l'intérieur des adultes. Le champignon *B. bassiana*, entomopathogène très efficace contre les coccinelles, n'a aucune prise sur la coccinelle asiatique aux États-Unis (Cottrell et Shapiro-Illan 2003). Un relâchement de la pression par les ennemis naturels (*enemy release hypothesis*; Keane et Crawley 2002) pourraient lui permettre d'atteindre de plus grandes densités de population et allouer les ressources ingérées à un meilleur développement plutôt qu'à la protection contre les ennemis naturels (*evolution of increased competitive ability*; Blossey et Nötzold 1995), ce qui lui conférerait un grand avantage sur les espèces natives.

Ce doctorat apporte ainsi des données plus complètes sur les différentes caractéristiques des espèces envahissantes, de leur lien avec la communauté et sur les caractéristiques de l'environnement qui peuvent affecter l'invasion d'une espèce. Ces données pourront être très utiles au domaine en croissance des invasions biologiques (Pimentel *et al.* 2005; Simberloff *et al.* 2005). Nous avons pu montrer que les caractéristiques des stades juvéniles doivent être prises en compte dans les études sur les espèces envahissantes car elles ont souvent une grande incidence sur le résultat de l'invasion. La survie de ces stades, souvent plus vulnérables au manque de ressource, à la compétition ou à la prédation, peut permettre ou non l'invasion de l'espèce. Afin de mieux comprendre les invasions biologiques, les études futures devraient intégrer l'étude plus en profondeur des stades juvéniles des différentes espèces envahissantes.

De plus, les études sur les invasions biologiques évaluent le plus souvent un niveau à la fois, ce qui ne donne pas un portrait global des mécanismes d'invasion et des impacts potentiels de cette invasion. Notre étude démontre bien l'importance d'étudier plus en profondeur l'équation espèce, communauté, environnement afin de mieux prédire l'évolution et les impacts des espèces envahissantes.

On peut se demander maintenant dans quelle direction la situation va-t-elle évoluer? Il est trop tôt encore pour dire que les populations de la coccinelle sont à l'équilibre avec le milieu. Par exemple, la coccinelle asiatique est la dernière espèce de coccinelle à entrer en hibernation; elle rejoint les maisons au mois d'octobre, lorsque les autres espèces sont déjà sur les sites d'hibernation depuis la fin du mois d'août ou le début septembre. Ce décalage la pousse à manger tout ce qui lui tombe sous la dent, que ce soit ses congénères, d'autres insectes ou même des fruits (voir Lucas *et al.* Annexe B). Avec le temps, nous devrions observer une diminution de ce décalage vers une hibernation plus tôt dans la saison. De plus, nous pouvons nous attendre à une évolution conjointe des parasitoïdes avec cette espèce. La coccinelle asiatique semble posséder des mécanismes immunitaires qui lui permettent de résorber ou d'éviter le développement des larves du parasitoïde *D. coccinellae* (Firlej, thèse de doctorat). Une évolution de ce parasitoïde vers de meilleures capacités à parasiter la coccinelle est à prévoir, vu que la coccinelle asiatique est prédominante dans l'habitat et que le parasitoïde a une préférence pour cet hôte (Firlej, thèse de doctorat). Un autre parasitoïde, *S. triangulifera*, est présent au Canada (O'Hara et Wood, 2004), et s'attaque à la coccinelle aux États-Unis (Katsoyannos et Aliniaze 1998), avec plus de succès de parasitisme que *D. coccinellae*. Nous n'avons pas observé de coccinelle asiatique parasitée par cette espèce, mais nous pouvons nous attendre à une augmentation du parasitisme lorsque ce parasitoïde aura développé une reconnaissance de cette nouvelle espèce. Les autres espèces de coccinelles et autres aphidiphages qui peuvent se nourrir des œufs et premiers stades larvaires de la coccinelle devraient aussi stabiliser les populations. Plusieurs espèces de coccinelles

sont présentes dans les champs avant la coccinelle asiatique et peuvent interférer avec les œufs et premiers stades, diminuant ainsi potentiellement les populations. Il devrait donc y avoir une stabilisation des populations par les ennemis naturels durant les prochaines années.

Au cours des 10 dernières années, la coccinelle asiatique a pris une grande place au sein des communautés aphidiphages. Quel sera l'impact à long terme sur les espèces indigènes? Malgré les nombreuses études qui relatent des effets négatifs de cette espèce en laboratoire ou quelquefois au champ (voir Lucas *et al.* Annexe B), nous supposons que la coexistence avec les espèces indigènes sera possible. Nos expériences ont démontré que la coccinelle maculée, bien que très similaire au niveau de la niche spatiale, coexistait dans toutes les situations avec la coccinelle asiatique. La coccinelle maculée est toutefois très plastique elle aussi, ce qui lui permet d'utiliser différentes ressources à divers endroits. Certaines espèces moins plastiques ou plus spécialisées vont être affectées par la coccinelle asiatique (Hoogendoorn et Heimpel 2004; Michaud 2003), mais probablement pas au point de les mener à l'extinction. Il semble que la coccinelle à sept points, plus aphidiphage et donc plus spécialisée, soit affectée par la présence de la coccinelle asiatique. Malgré le fait que ces deux espèces de coccinelles se côtoient dans leur milieu d'origine (Hironori et Katsuhiko 1997), des observations aux États-Unis ont montré une certaine diminution ou une disparition de cette espèce dans des vergers où la coccinelle asiatique était présente (Brown et Miller 1998; Colunga-Garcia et Gage 1998). Cependant, la forte incidence de cannibalisme de la coccinelle asiatique semble stabiliser la chaîne alimentaire et permettre une coexistence avec les autres espèces. Des suivis de population devront toutefois être entrepris à plus long terme afin d'obtenir une réponse claire à ce sujet.

Ce doctorat nous mène à un sérieux questionnement quant à l'introduction d'espèces exotiques pour la lutte biologique classique. La coccinelle asiatique était un

excellent candidat pour le contrôle biologique de plusieurs espèces de pucerons. Elle est encore vendue comme agent de lutte biologique à plusieurs endroits dans le monde. C'est une espèce qui semble faire un bon contrôle biologique des pucerons, sans perturber le contrôle par les autres espèces (voir Lucas *et al.* Annexe B; Tableau 1). Cette espèce peut s'attaquer cependant à d'autres espèces qui ne font pas partie de la guilde aphidiphage, comme par exemple le monarque, *Danaus plexippus* L. (Koch *et al.* 2003; 2005) ou bien une espèce de galéruque, *Galerucella californiensis* L. (Coleoptera : Chrysomelidae), utilisé pour le contrôle biologique de la salicaire pourpre (Sebolt et Landis 2004). Les impacts ne sont pas seulement dans le milieu naturel. L'utilisation des maisons comme site d'hibernation cause des allergies chez certaines personnes (Yarbrough *et al.* 1999), des mauvaises odeurs, les gens se font mordre par la coccinelle et sa présence devient très inconfortable (Kovach 2004; voir Lucas *et al.* Annexe B, Tableau 4). Elle se nourrit aussi des fruits endommagés à l'automne, lorsqu'il n'y a plus de nourriture. Ce comportement est très problématique pour l'industrie vinicole, car seulement une dizaine de coccinelle asiatique récoltés en même temps que le raisin gâche le goût du vin (Kovach 2004; Pickering *et al.* 2004). Ainsi, les impacts négatifs occasionnés par cette espèce sont assez importants pour recommander des études plus approfondies avant d'introduire une nouvelle espèce généraliste dans un nouvel environnement.

L'intérêt de cette étude était autant appliqué que fondamental. De façon appliquée, nous avons pu mesurer certains impacts de la coccinelle asiatique sur les communautés et sur les humains. Au niveau plus fondamental, nous avons déterminé les mécanismes d'invasion de cette espèce, qui pourront servir de modèle pour l'étude d'autres espèces envahissantes, afin de prévenir ou de comprendre ces invasions. L'arrivée de la coccinelle asiatique au Québec était une opportunité fantastique d'étudier une nouvelle espèce dans un nouveau milieu, avec toute la complexité des interactions avec la communauté et l'environnement.

BIBLIOGRAPHIE GÉNÉRALE

- Abrams, P.A. (2001) The effect of density-independent mortality on the coexistence of exploitative competitors for renewing resources. *American Naturalist*, **158**, 459-470.
- Adriaens, T., Branquart, E. et Maes, D. (2003) The multicolored asian ladybird *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), a threat for native aphid predators in Belgium? *Belgian Journal of Zoology*, **133**, 195-196.
- Agarwala, B.K., Bardhanroy, P., Yasuda, H. et Takizawa, T. (2001) Prey consumption and oviposition of the aphidophagous predator *Menochilus sexmaculatus* (Coleoptera : Coccinellidae) in relation to prey density and adult size. *Environmental Entomology*, **30**, 1182-1187.
- Agarwala, B.K. et Bhattacharya, S. (1995) Adaptive features of the predatory ladybird beetles in uncertain and competitive habitats. *Current Science*, **69**, 587-591.
- Agarwala, B.K. et Dixon, A.F.G. (1992) Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecological Entomology*, **17**, 303-309.
- Agarwala, B.K., Yasuda, H. et Kajita, Y. (2003) Effect of conspecific and heterospecific feces on foraging and oviposition of two predatory ladybirds: role of fecal cues in predator avoidance. *Journal of Chemical Ecology*, **29**, 357-376.
- Alyokhin, A. et Sewell, G. (2004) Changes in a lady beetle community following the establishment of three alien species. *Biological Invasions*, **6**, 463-471.
- Ancel Meyers, L. et Bull, J.J. (2002) Fighting change with change: adaptive variation in an uncertain world. *Trends in Ecology and Evolution*, **17**, 551-557.
- Agence Canadienne d'Inspection des Aliments (ACIA). (2004) Plan d'action proposé pour les plantes terrestres et les phytoravageurs étrangers envahissants. Phase 1. Ottawa, Canada.
- Angalet, G.W., Tropp, J.M. et Eggert, A.N. (1979) *Coccinella septempunctata* in the United States : recolonizations and notes on its ecology. *Environmental Entomology*, **8**, 896-901.
- Arim, M. et Marquet, P.A. (2004) Intraguild predation: a widespread interaction related to species biology. *Ecology Letters*, **7**, 557-564.
- Balciunas, D. et Lawler, S.P. (1995) Effects of basal resources, predation, and alternative prey in microcosm food chains. *Ecology* **76**, 1327-1336.
- Bale, J.S. (1987) Insect cold hardiness: freezing and supercooling - an ecological perspective. *Journal of Insect Physiology*, **33**, 899-908.

- perspective. *Journal of Insect Physiology*, **33**, 899-908.
- Bale, J.S. (1991) Insects at low temperature: a predictable relationship? *Functional Ecology*, **5**, 291-298.
- Bando, K.J. (2006) The roles of competition and disturbance in a marine invasion. *Biological Invasions*, **8**, 755-763.
- Bazzochi, G.G., Lanzoni, A., Accinelli, G. et Burgio, G. (2004) Overwintering, phenology and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. *BioControl*, **49**, 245-260.
- Begon, M., Harper, J.L. et Townsend, C.R. (1996). *Ecology: individuals, populations, and communities*. Boston, Blackwell Science.
- Benton, A.H. et Crump, A.J. (1979) Observations on aggregation and overwintering in the coccinellid beetle *Coleomegilla maculata* (DeGeer). *New York Entomological Society*, **87**, 154-159.
- Blossey, B. et Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-889.
- Bohannan, B. J. M. and Lenski, R. E. (1999) Effect of prey heterogeneity on the response of a model food chain to resource enrichment. *American Naturalist* **153**, 73-82.
- Brown, M.W. (2003) Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl*, **48**, 141-153.
- Brown, M.W. et Miller, S.S. (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News*, **109**, 143-151.
- Burgio, G., Santi, F. et Maini, S. (2002) On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). *Biological Control*, **24**, 110-116.
- Burke, M. J. W., et Grime, J. P. (1996) An experimental study of plant community invasibility. *Ecology* **77**, 776-790.
- Burley, L.A., Moyer, A.T. et Petranka, J.W. (2006) Density of an intraguild predator mediates feeding group size, intraguild egg predation, and intra- and interspecific competition. *Oecologia*, **148**, 641-649.
- Butler, G.D. (1982) Development time of *Coccinella septempunctata* in relation to constant temperatures (Col.: Coccinellidae). *Entomophaga*, **27**, 349-353.
- Byers, J.E. (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos*, **97**, 449-458.
- Byers, J.E. (2000) Competition between two estuarine snails: implications for

- invasions of exotic species. *Ecology*, **81**, 1225-1239.
- Byers, J.E. et Goldwasser, L. (2001) Exposing the mechanism and timing of impact of nonindigenous species on native species. *Ecology*, **82**, 1330-1343.
- Caltagirone, L.E. (1981) Landmark examples in classical biological control. *Annual Review of Entomology*, **26**, 213-232.
- Caltagirone, L.E. et Douthett, R.L. (1989) The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology*, **34**, 1-16.
- Carpenter, D. et Cappucino, N. (2005) Herbivory, time since introduction and the invasiveness of exotic plants. *Journal of Ecology*, **93**, 315-321.
- Ceryngier, P. (2000) Overwintering of *Coccinella septempunctata* (Coleoptera: Coccinellidae) at different altitudes in the Karkonosze Mts, SW Poland. *European Journal of Entomology*, **97**, 323-328.
- Ceryngier, P. et Hodek, I. (1996). Enemies of Coccinellidae. Dans Hodek, I. et Honěk, A. (Eds) *Ecology of Coccinellidae*. Dordrecht/Boston/London, Kluwer Academic Publisher. pp. 319-350.
- Chapin, J.B. et Brou, V.A. (1991) *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, **93**, 630-635.
- Chase, J.M. (1999) Food web effects of prey size refugia: variable interactions and alternative stable equilibria. *American Naturalist*, **154**, 559-570.
- Chase, J.M. (1996) Abiotic controls of trophic cascade in a simple grassland food chain. *Oikos*, **77**, 495-506.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**, 343-366.
- Coderre, D. (1983) *Écologie des espèces aphidiennes aphidiphages inféodées au maïs de la région sud du Québec*. Thèse de doctorat, Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada.
- Coderre, D., Lucas, É. et Gagné, I. (1995) The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) in Canada. *Canadian Entomologist*, **127**, 609-611.
- Coderre, D., Provencher, L. et Tourneur, J.-C. (1987) Oviposition and niche partitioning in aphidophagous insects on maize. *Canadian Entomologist*, **119**, 195-203.
- Colautti, R.I., Bailey, S.A., van Overdijk, C.D.A., Amundsen, K. et MacIsaac, H.J. (2006) Characterised and projected costs of nonindigenous species in Canada.

Biological Invasions, **8**, 45-59.

- Colautti, R.I., Muirhead, J.R., Biswas, R.N. et MacIsaac, H.J. (2005) Realized vs apparent reduction in enemies of the European starling. *Biological Invasions*, **7**, 723-732.
- Colunga-Garcia, M. et Gage, S.H. (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology*, **27**, 1574-1580.
- Connell, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, **35**, 131-138.
- Corbin, J.D. et D'Antonio, C.M. (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology*, **85**, 1273-1283.
- Costanzo, K.S., Desavaraju, B. et Juliano, S.A. (2005) Condition-specific competition in container mosquitoes: the role of noncompeting life-history stages. *Ecology*, **86**, 3289-3295.
- Cottrell, T.E. (2004) Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biological Control*, **31**, 362-371.
- Cottrell, T.E. et Shapiro-Ilan, D.I. (2003) Susceptibility of a native and an exotic lady beetle (Coleoptera: Coccinellidae) to *Beauveria bassiana*. *Journal of Invertebrate Pathology*, **84**, 137-144.
- Cottrell, T.E. et Yeargan, K.V. (1999) Factors influencing dispersal of larval *Coleomegilla maculata* from the weed *Acalypha ostryaefolia* to sweet corn. *Entomologia Experimentalis et Applicata*, **90**, 313-322.
- Cottrell, T.E. et Yeargan, K.V. (1998a) Effect of pollen on *Coleomegilla maculata* (Coleoptera : Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology*, **27**, 1402-1410.
- Cottrell, T.E. et Yeargan, K.V. (1998b) Influence of a native weed, *Acalypha ostryaefolia* (Euphorbiaceae), on *Coleomegilla maculata* (Coleoptera : Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology*, **27**, 1375-1385.
- Cottrell, T.E. et Yeargan, K.V. (1998c) Intraguild predation between an introduced lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Journal of Kansas Entomological Society*, **71**, 159-163.
- Dawson, M. (2002) Plant quarantine: a tool for preventing the introduction and spread of alien species harmful to plants. Dans Claudi, R., Nantel, P. et Muckle-Jeffs, E.

- (eds) *Alien invaders in Canada's waters, wetlands and forests*. Canadian Forest Service, Ottawa, Canada. pp. 243-251.
- Day, W.H., Prokrym, D.R., Ellis, D.R. et Chianese, R.J. (1994) The known distribution of the predator *Propylea-quatuordecimpunctata* (Coleoptera, Coccinellidae) in the United States, and thoughts on the origin of this species and 5 other exotic lady beetles in Eastern North-America. *Entomological News*, **105**, 244-256.
- de Almeida, L.M. et da Silva, V.B. (2002) Primeiro registro de *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae): um coccinelideo originario da regio Paleartica. *Revista Brasileira Zoologica*, **19**, 941-944.
- DeBach, P. et Rosen, D. (1991) *Biological control by natural enemies*, Cambridge University Press, New York.
- DeClercq, P., Peeters, I., Vergauwe, G. et Thas, O. (2003) Interaction between *Podisus maculiventris* and *Harmonia axyridis*, two predators used in augmentative biological control in greenhouse crops. *BioControl*, **48**, 39-55.
- Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M. et Gemmell, N.J. (2005). Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution*, **20**, 470-474.
- Diehl, S. et Feissel, M. (2000) Effects of enrichment on three-level food chains with omnivory. *American Naturalist*, **155**, 200-218.
- Diehl, S. et Feissel, M. (2001) Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. *Ecology*, **82**, 2977-2983.
- Dixon A.F.G. (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia bipunctata* (L.) *Journal of Animal Ecology* **28**, 259-281.
- Dixon, A.F.G. (2000). *Insect predator-prey dynamics: ladybird beetles and biological control*. Cambridge, Cambridge University Press.
- Dixon, A.F.G. et Hemptinne, J.L. (2001) Body size distribution in predatory ladybird beetles reflects that of their prey. *Ecology*, **82**, 1847-1856.
- Dixon, A.F.G. et Stewart, L.A. (1991) Size and foraging in ladybird beetles. In Polgar, L., Chambers, R.J., Dixon, A.F.G. and Hodek, I. (Eds) *Behaviour and impacts of Aphidophaga*. SPB Academic Publishing bv, The Hague, The Netherlands. p. 123-132.
- Dixon, A.F.G. et Guo, Y. (1993) Egg and cluster size in ladybird beetles (Coleoptera: Coccinellidae): the direct and indirect effects of aphid abundance. *European Journal of Entomology*, **90**, 457-463.
- Drake, J.A., Mooney, H.A., diCastri, F., Groves, R.H., Kruger, F.J., Rejmanek, M. et

- Williamson, M. (1989) *Biological invasions: a global perspective*. SCOPE, John Wiley and Sons Ltd.
- Dreistadt, S.H., Hagen, K.S. et Bezark, L.G. (1995) *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae), First Western United States record for this asiatic Lady beetle. *Pan-Pacific Entomologist*, **71**, 135-136.
- Dudgeon, S.R., Steneck, R.S., Davison, I.R. et Vadas, R.L. (1999) Coexistence of similar species in a space-limited intertidal zone. *Ecological Monographs*, **69**, 331-352.
- Dukes, J.S. et Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology and Evolution*, **14**, 135-139.
- Ehler, L.E. (1998) Invasion biology and biological control. *Biological Control*, **13**, 127-133.
- Elliott, N., Kieckhefer, R. et Kauffman, W. (1996) Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia*, **105**, 537-544.
- Elliott, N. C. et Kieckhefer, R. W. (1990) A thirteen-year survey of the aphidophagous insects of alfalfa. *Prairie Naturalist*, **22**, 87-96.
- Ellis, D.R., Prokrym, D.R. et Adams, R.G. (1999) Exotic lady beetle survey in northeastern United States: *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Entomological News*, **110**, 73-84.
- Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Environment Canada (2006) Climate data online. http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_f.html.
- Ettifouri, M. et Ferran, A. (1993) Influence of larval rearing diet on the intensive searching behaviour of *Harmonia axyridis* (Col: Coccinellidae) larvae. *Entomophaga*, **38**, 51-59.
- Evans, E.W. (2004) Habitat displacement of North American ladybirds by an introduced species. *Ecology*, **85**, 637-647.
- Evans, E.W. (1991) Intra versus interspecific interactions in ladybeetles (Coleoptera: Coccinellidae) attacking aphids. *Oecologia*, **87**, 401-408.
- Evans, E.W. et Dixon, A.F.G. (1986) Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. *Journal of Animal Ecology* **55**, 1027-1034.
- Félix, S. et Soares, A.O. (2004) Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of body weight. *European Journal of*

- Entomology*, **101**, 237-242.
- Finke, D.L. et Denno, R.F. (2002) Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology*, **83**, 643-652.
- Firlej, A., Boivin, G., Lucas, É. et Coderre, D. (2005) First report of *Harmonia axyridis* Pallas being attacked by *Dinocampus coccinellae* Schrank in Canada. *Biological Invasions*, **7**, 553-556.
- Formusoh, E. S. et Wilde, G. E. (1993) Preference and development of two species of predatory coccinellid on the Russian wheat aphid and greenbug biotype E (Homoptera : Aphididae). *Journal of Agricultural Entomology* **10**, 65-70.
- Fox, T.B., Landis, D.A., Cardoso, F.F. et Difonzo, C.D. (2005) Impact of predation on establishment of the soybean aphid, *Aphis glycines* in soybean, *Glycine max*. *BioControl*, **50**, 545-563.
- Fréchette, B., Alauzet, C. et Hemptinne, J.-L. (2003). *Oviposition behaviour of the two-spot ladybird beetle Adalia bipunctata (L.) (Coleoptera: Coccinellidae) on plants with conspecific larval tracks*. Proceeding of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidiphagous Insects., Azores, Arquipélago-Life and Marine Science.
- Fréchette, B., Dixon, A.F.G., Alauzet, C. et Hemptinne, J.-L. (2004) Age and experience influence patch assessment for oviposition by an insect predator. *Ecological Entomology*, **29**, 578-583.
- Fréchette, B., Rojo, S., Alomar, O. et Lucas, É. (2007) Intraguild predation between syrphids and mirids : Who is the prey ? Who is the predator? *BioControl*, **52**, 175-191.
- Gordon, R.D. (1987) The first North American records of *Hippodamia variegata* (Goeze) (Coleoptera : Coccinellidae). *Journal of the New York Entomological Society*, **95**, 307-309.
- Gordon, R.D. et Vandenberg, N. (1991) Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. *Proceedings of the Entomological Society of Washington*, **93**, 845-864.
- Gordon, R.D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of New York Entomological Society*, **93**, 1-912.
- Grill, C.P., Moore, A.J., Brodie, E.D. III. (1997) The genetics of phenotypic plasticity in a colonizing population of the ladybird, *Harmonia axyridis*. *Heredity*, **78**, 261-269.
- Grosholz, E. (2002) Ecological and evolutionary consequences of coastal invasions.

Trends in Ecology and Evolution, **17**, 22-27.

- Gustafson, M.P. (1993) Intraguild predation among larval plethodontid salamanders - a field experiment in artificial stream pools. *Oecologia*, **96**, 271-275.
- Hagley, E.A.C. (1999). *Predatory insects in fruit orchards in Southern Ontario*. Publication 208 Agriculture and Agri-Food Canada and Ontario Ministry of Agriculture, Food and Rural Affairs.
- Hall, R.W., Ehler, L.E. et Bisabri-Ershadi, B. (1980) Rate of success in classical biological control of arthropods. *Entomological Society of America Bulletin*, **26**, 111-114.
- Hänfling, B. et Kollmann, J. (2002) An evolutionary perspective of biological invasion. *Trends in Ecology and Evolution*, **17**, 545-546.
- Hanski, I. 1989. Does it help to have more of the same? *Trends in Ecology and Evolution*, **4**: 113-114.
- Harwood, J.D., Ricci, C., Romani, R., Pitz, K.M., Weir, A. et Obrycki, J. (2006) Prevalence and association of the laboulbenialean fungus *Hesperomyces virescens* (Laboulbeniales: Laboulbeniaceae) on coccinellid hosts (Coleoptera: Coccinellidae) in Kentucky, USA. *European Journal of Entomology*, **103**, 799-804.
- Hemptinne, J.L., Lognay, G., Gauthier, C. et Dixon, A.F.G. (2000) Role of surface chemical signals in egg cannibalism and intraguild predation in ladybirds (Coleoptera : Coccinellidae). *Chemoecology*, **10**, 123-128.
- Hemptinne, J.-L., Dixon, A.F.G. et Coffin, J. (1992) Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia*, **90**, 238-245.
- Hierro, J.L., Maron, J.L. et Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5-15.
- Hindayana, D., Meyhöfer, R., Scholz, D. et Poehling, H.-M. (2001) Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. *Biological Control* **20**, 236-246.
- Hironori, Y. et Katsuhiko, S. (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga*, **42**, 153-163.
- Hodek, I. (1973). *Biology of Coccinellidae*. The Hague, Prague, Dr. W. Junk N. V., Publishers.

- Hodek, I. et Honěk, A. (1996). *Ecology of Coccinellidae*. Netherlands, Kluwer Academic Publishers.
- Hoebeker, E.R. et Wheeler, A.G.Jr. (1996) Adventive lady beetles (Coleoptera:Coccinellidae) in the Canadian Maritime Provinces, with new eastern U.S.records of *Harmonia quadripunctata*. *Entomological News*, **107**, 281-290.
- Holt, R.D. et Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, **25**, 495-520.
- Holt, R.D. et Polis, G.A. (1997) A theoretical framework for intraguild predation. *American Naturalist*, **149**, 745-764.
- Holway, D.A. (1998) Factors governing rate of invasion - a natural experiment using Argentine ants. *Oecologia*, **115**, 206-212.
- Holway, D.A. (1999) Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology*, **80**, 238-251.
- Holway, D.A. et Case, T.J. (2001) Effects of colony-level variation on competitive ability in the invasive Argentine ant. *Animal Behaviour*, **61**, 1181-1192.
- Holway, D.A. et Suarez, A.V. (1999) Animal behavior: an essential component of invasion biology. *Trends in Ecology and Evolution*, **14**, 328-330.
- Honěk, A. (1989) Overwintering and annual changes of abundance of *Coccinella septempunctata* in Czechoslovakia (Coleoptera, Coccinellidae). *Acta Entomologica Bohemoslovaca*, **86**, 179-192.
- Honěk, A. (1997) Factors determining winter survival in *Coccinella septempunctata* (Col., Coccinellidae). *Entomophaga*, **42**, 119-124.
- Hood, W.G. et Naiman, R.J. (2000) Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecology*, **148**, 105-114.
- Hoogendoorn, M. et Heimpel, G.E. (2002) Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. *Biological Control*, **25**, 224-230.
- Hoogendoorn, M. et Heimpel, G.E. (2004) Competitive interactions between an exotic and a native ladybeetle: a field cage study. *Entomologia Experimentalis et Applicata*, **111**, 19-28.
- Huelsman, M.F., Jasinski, J., Young, C. et Kovach, J. (2001) The multicolored Asian lady beetle *Harmonia axyridis*: a nuisance pest in Ohio. <http://ipm.osu.edu/lady/icup.htm>
- Huey, D.H. (1966). *Kingzett's chemical encyclopedia: a digest of chemistry and industrial application*. William Clowes, London.

- Hui, C., Li, Z. et Yue, D.-X. (2004) Metapopulation dynamics and distribution, and environmental heterogeneity induced by niche construction. *Ecological Modelling*, **177**, 107-118.
- Iablokoff-Khnzorian, S.M. (1982). *Les coccinelles, Coléoptères-Coccinellidae*. Société Nouvelle des Éditions Boubée, Paris.
- Jean, C., Coderre, D. et Tourneur, J.-C. (1990) Effects of temperature and substrate on survival and lipid consumption of hibernating *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae). *Environmental Entomology*, **19**, 1657-1662.
- Kajita, Y., Takano, F., Yasuda, H. et Agarwala, B.K. (2000) Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. *Applied Entomology and Zoology*, **35**, 473-479.
- Katsoyannos, P. et Aliniaze, M.T. (1998) First record of *Strongygaster triangulifera* (Loew) (Diptera : Tachinidae) as a parasitoid of *Harmonia axyridis* (Pallas) (Coleoptera : Coccinellidae) in western North America. *Canadian Entomologist*, **130**, 905-906.
- Keane, R.M. et Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164-170.
- Kidd, K.A. et Nalepa, C.A. (1995) Distribution of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in North Carolina and Virginia. *Proceedings of the Entomological Society of Washington*, **97**, 729-731.
- Kieckhefer, R.W., Elliott, N.C. et Beck, D.A. (1992) Aphidophagous coccinellids in alfalfa, small grains, and maize in eastern South Dakota. *Great Lakes Entomologist*, **25**, 15-23.
- Kiesecker, J.M., Blaustein, A.R. et Miller, C.L. (2001) Potential mechanisms underlying the displacement of native red-legged frogs by introduced bullfrogs. *Ecology*, **82**, 1964-1970.
- Kimberling, D.N. (2004) Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. *Biological Invasions*, **6**, 301-318.
- Kindlmann, P. et Dixon, A.F.G. (1993) Optimal foraging in ladybird beetles (Coleoptera, Coccinellidae) and its consequences for their use in biological control. *European Journal of Entomology*, **90**, 443-450.
- Knick, S.T. et Rotenberry, J.T. (1997) Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho. *Landscape Ecology*, **12**, 287-297.
- Koch, R.L. (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of*

Insect Science, **3**, 1-16.

- Koch, R.L., Hutchison, W.D., Venette, R.C. et Heimpel, G.E. (2003) Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biological Control*, **28**, 265-270.
- Koch, R.L., Carrillo, M.A., Venette, R.C., Cannon, C.A. et Hutchison, W.D. (2004) Cold hardiness of the multicolored Asian lady beetle (Coleoptera: Coccinellidae). *Environmental Entomology*, **33**, 815-822.
- Koch, R.L., Venette, R.C. et Hutchison, W.D. (2005) Influence of alternate prey on predation of monarch butterfly (Lepidoptera: Nymphalidae) larvae by the multicoloured Asian lady beetle (Coleoptera: Coccinellidae). *Environmental Entomology*, **34**, 410-416.
- Kolar, C.S. et Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199-204.
- Kotler, B.P. et Brown, J.S. (1988) Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* **19**, 281-307
- Kovach, J. (2004) Impact of multicolored Asian lady beetles as a pest of fruit and people. *American Entomologist*, **50**, 159-161.
- Kozlowski, J. et Wiener, J. (1997) Interspecific allometries are by-products of body size optimization. *The American Naturalist*, **149**, 352-380.
- Krafsur, E.S., Obrycki, J.J. et Harwood, J.D. (2005) Comparative genetic studies of native and introduced Coccinellidae in North America. *European Journal of Entomology*, **102**, 469-474.
- Krafsur, E.S., Kring, T.J., Miller, J.C., Nariboldi, P., Obrycki, J.J., Ruberson, J.R. et Schaefer, P.W. (1997) Gene flow in the exotic colonizing ladybeetle *Harmonia axyridis* in North America. *Biological Control*, **8**, 207-214.
- Krijger, C.L., Peters, Y.C. et Sevenster, J.G. (2001) Competitive ability of neotropical *Drosophila* predicted from larval development times. *Oikos*, **92**, 325-332.
- Krivan, V. et Diehl, S. (2005) Adaptive omnivory and species coexistence in tri-trophic food webs. *Theoretical Population Biology*, **67**, 85-99.
- Labrie, Coderre, D. et Lucas, É. (2007) Overwintering strategy of the multicolored Asian ladybeetle (Coleoptera: Coccinellidae): a cold-free space as a factor of invasive success. *Annals of the Entomological Society of America*, **in press**.
- Labrie, G., Lucas, É. et Coderre, D. (2006) Can developmental and behavioral characteristics of the multicolored Asian lady beetle *Harmonia axyridis*

- explain its invasive success? *Biological Invasion*, **8**, 743-754.
- LaMana, M.L. et Miller, J.C. (1996) Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biological Control*, **6**, 232-237.
- Lambrinos, J.G. (2006) Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass. *Oecologia* **147**, 327-334.
- Lanzoni, A., Accinelli, G., Bazzocchi, G.G. et Burgio, G. (2004) Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Col. Coccinellidae). *Journal of Applied Entomology*, **128**, 298-306.
- Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends in Ecology and Evolution*, **17**, 386-391.
- Levine, J.M. et D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15-26.
- Levine, J.M. Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. et Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B*, **270**, 775-781.
- Lima, S.L. et Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.
- Lodge, D.M. (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution*, **8**, 133-137.
- Lodge, D.M., Williams, S.L., MacIsaac, H.J., Hayes, K., Leung, B., Reichard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., Carlton, J.T. et McMichael, A. (2006) Biological invasions: recommendations for U.S. policy and management.
- Long, J.L. (1981) *Introduced Birds of the World*. UniverseBooks, New York.
- Lounibos, L.P., O'Meara, G.F., Escher, R.L., Nishimura, N., Cutwa, M., Nelson, T., Campos, R.E. et Juliano, S.A. (2001) Testing predictions of displacement of native *Aedes* by the invasive Asian tiger mosquito *Aedes albopictus* in Florida, USA. *Biological Invasions*, **3**, 151-166.
- Lucas, É. (2005) Intraguild predation among aphidophagous predators. *European Journal of Entomology*, **102**, 351-364.
- Lucas, E. et Alomar, O. (2002a) Impact of *Macrolophus caliginosus* presence on damage production by *Dicyphus tamaninii* (Heteroptera: Miridae) on tomato fruits. *Journal of Economic Entomology*, **95**, 1123-1126.

- Lucas, E. et Alomar, O. (2002b) Impact of the presence of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on whitefly (Homoptera: Aleyrodidae) predation by *Macrolophus caliginosus* (Wagner) (Heteroptera: Miridae). *Biological Control*, **25**, 123-128.
- Lucas, É. et Brodeur, J. (1999) Oviposition site selection by the predatory midge *Aphidoletes aphidimyza* (Diptera : Cecidomyiidae). *Environmental Entomology*, **28**, 622-627.
- Lucas, É., Labrie, G., Vincent, C. et Kovach, J. (2007). The multicolored Asian ladybeetle, *Harmonia axyridis* - beneficial or nuisance organism? Dans Vincent, C., Goettel, M. et Lazarovitz, G. (Eds) *Case studies in biological control: a global perspective*. UK, CABI Publishing. Sous presse.
- Lucas, É., Gagné, I. et Coderre, D. (2002) Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **99**, 457-463.
- Lucas, É., Coderre, D. et Brodeur, J. (2000) Selection of molting and pupation sites by *Coleomegilla maculata* (Coleoptera: Coccinellidae): avoidance of intraguild predation. *Environmental Entomology*, **29**, 454-459.
- Lucas, É., Coderre, D. et Brodeur, J. (1998a) Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology*, **79**, 1084-1092.
- Lucas, É., Lapalme, S. et Coderre, D. (1998b) Voracité comparative de trois coccinelles prédatrices contre le tétranyque rouge du pommier (Acarina: Tetranychidae). *Phytoprotection*, **78**, 117-123.
- Lucas, É., Coderre, D. et Vincent, C. (1997a) Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. *Entomologia Experimentalis et Applicata*, **85**, 151-159.
- Lucas, É., Coderre, D. et Brodeur, J. (1997b) Instar-specific defense of *Coleomegilla maculata lengi* (Col.: Coccinellidae): influence on attack success of the intraguild predator *Chrysoperla rufilabris* (Neur.: Chrysopidae). *Entomophaga*, **42**, 3-12.
- MacDougall, A.S. et Turkington, R. (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, **86**, 42-55
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. et Bazzaz, F.A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689-710.
- Majerus, M., Strawson, V. et Roy, H. (2006) The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera:

- Coccinellidae), in Britain. *Ecological Entomology*, **31**, 207-215.
- Majerus, M.E.N. (1994). *Ladybirds*. London, Harper Collins.
- Majerus, M.E.N. (1997) How is *Adalia bipunctata* (Linn.) attracted to overwintering sites? *Entomologist*, **116**, 212-217.
- Marco, D.E., Paez, S.A. et Cannas, S.A. (2002) Species invasiveness in biological invasions: a modelling approach. *Biological Invasions*, **4**, 193-205.
- McClure, M.S. (1987) Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* bean and godwin (Homoptera: Margarodidae) in the United States. *Environmental Entomology*, **16**, 224-230.
- McClure, M.S. (1986) Importing ladybird beetles to control red pine scale. *Frontiers of Plant Science*, **39**, 5-7.
- McCorquodale, D.B. (1998) Adventive lady beetles (Coleoptera : Coccinellidae) in Eastern Nova Scotia, Canada. *Entomological News*, **109**, 15-20.
- McCutcheon, T.W. et Scott, H.R. Observation of cosmetic damage on a house caused by the multicolored asian lady beetle, *Harmonia axyridis* (Coleoptera, Coccinellidae). West Virginia University Extension Service.
- McPeck, M.A. (2004) The growth/predation risk trade-off: so what is the mechanism? *American Naturalist*, **163**, E88-E111.
- Menge, B.A. et Sutherland, J.P. (1976) Species diversity gradients: ;synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist*, **110**, 351-369.
- Michaud, J.P. (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. *Environmental Entomology*, **31**, 827-835.
- Michaud, J.P. (2003) A comparative study of larval cannibalism in three species of ladybird. *Ecological Entomology*, **28**, 92-101.
- Michaud, J.P. et Grant, A.K. (2003) Intraguild predation among ladybeetles and a green lacewing: do the larval spines of *Curinus coeruleus* (Coleoptera: Coccinellidae) serve a defensive function? *Bulletin of Entomological Research*, **93**.
- Mignault, M.-P., Roy, M. et Brodeur, J. (2006) Soybean aphid predators in Québec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *BioControl*, **51**, 89-106.
- Mills, N.J. (1982) Voracity, cannibalism and coccinellid predation. *Journal of Applied Biology*, **101**, 144-148.

- Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K. et Relyea, R.A. (2005) Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution*, **20**, 685-692.
- Minoretti, N. et Weisser, W.W. (2000) The impact of individual ladybirds (*Coccinella septempunctata*, Coleoptera : Coccinellidae) cell aphid colonies. *European Journal of Entomology*, **97**, 475-479.
- Mooney, H.A. et Cleland, E.E. (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 5446-5451.
- Morin, P. (1999) Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology*, **80**, 752-760.
- Müller, C.B. et Brodeur, J. (2002) Intraguild predation in biological control and conservation biology. *Biological Control*, **25**, 216-223.
- Müller, C.B. et Godfray, H.C.J. (1999) Indirect interactions in aphid-parasitoid communities. *Researches on Population Ecology*, **41**, 93-106.
- Munyaneza, J. et Obrycki, J.J. (1998a) Development of three populations of *Coleomegilla maculata* (Coleoptera, Coccinellidae) feeding on eggs of Colorado potato beetle (Coleoptera, Chrysomelidae). *Environmental Entomology*, **27**, 117-122.
- Munyaneza, J. et Obrycki, J.J. (1998b) Searching behavior of *Coleomegilla maculata* larvae feeding on Colorado potato beetle eggs. *Biological Control*, **13**, 85-90.
- Musser, F.R. et Shelton, A.M. (2003) Factors altering the temporal and within-plant distribution of coccinellids in corn and their impact on potential intraguild predation. *Environmental Entomology*, **32**, 575-583.
- Mylius, S.D., Klumpers, K., de Roos, A.M. et Persson, L. (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist*, **158**, 259-276.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. et Gale, S. (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, **91**, 97-108.
- Nalepa, C.A., Kennedy, G.G. et Brownie, C. (2005) Role of visual contrast in the alighting behavior of *Harmonia axyridis* (Coleoptera: Coccinellidae) at overwintering sites. *Environmental Entomology*, **34**, 425-431.
- Nalepa, C.A., Kidd, K.A. et Ahlstrom, K.R. (1996) Biology of *Harmonia Axyridis* (Coleoptera, Coccinellidae) in Winter Aggregations. *Annals of the Entomological Society of America*, **89**, 681-685.

- Nault, B.A. et Kennedy, G.G. (2003) Establishment of multicolored Asian lady beetle in Eastern North Carolina: seasonal abundance and crop exploitation within an agricultural landscape. *BioControl*, **48**, 363-378.
- Nedved, O. (1993) Comparison of cold hardiness in two ladybird beetles (Coleoptera: Coccinellidae) with contrasting hibernation behaviour. *European Journal of Entomology*, **90**, 465-470.
- Nedved, O. et Windsor, D. (1994) Supercooling ability, fat and water contents in a diapausing tropical beetle, *Stenotarsus rotundus* (Coleoptera: Endomychidae). *European Journal of Entomology*, **91**, 307-312.
- Noldus Information Technology b.v. 1989, 1990. The Observer 2.0. University Business and Technology Center, The Netherlands.
- Obata, S. (1986) Determination of hibernation site in the ladybird beetle, *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae). *Kontyu*, **54**, 218-223.
- Obata, S., Johki, Y. et Hidaka, T. (1986) Location of hibernation sites in the ladybird beetle *Harmonia axyridis*. Dans Hodek, I. (Ed.) *Ecology of Aphidophaga*. Dordrecht, Academia, Prague and Dr. W. Junk, pp. 193-198.
- Obrycki, J.J. et Kring, T.J. (1998) Predaceous coccinellidae in biological control. *Annual Review of Entomology*, **43**, 295-321.
- Obrycki, J. J. et Tauber, M. J. (1978) Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasite *Perilitus coccinellae* (Hymenoptera: Braconidae). *Canadian Entomologist*, **110**, 407-412.
- Obrycki, J.J., Giles, K.L. et Ormord, A.M. (1998) Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia*, **117**, 279-285.
- O'Hara, J.E. et Wood, D.M. (2004) Catalogue of the Tachinidae (Diptera) of America north of Mexico. *Memoirs on Entomology, International*, **18**, 410 pp.
- Okuyama, T. (2002) The role of antipredator behavior in an experimental community of jumping spiders with intraguild predation. *Population Ecology*, **44**, 121-125.
- Omkar, et Srivastava, S. (2003) Influence of six aphid prey species on development and reproduction of a ladybird beetle, *Coccinella septempunctata*. *BioControl*, **48**, 379-393.
- Osawa, N. (2003) The influence of female oviposition strategy on sibling cannibalism in the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **100**, 43-48.

- Osawa, N. (2001) The effect of hibernation on the seasonal variations in adult body size and sex ratio of the polymorphic ladybird beetle *Harmonia axyridis*: the role of thermal melanism. *Acta Societas Zoologicae Bohemicae*, **65**, 269-278.
- Osawa, N. (2000) Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera : Coccinellidae): resource tracking and population characteristics. *Population Ecology*, **42**, 115-127.
- Osawa, N. (1993) Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life table and key factor analysis. *Researches in Population Ecology*, **35**, 335-348.
- Osawa, N. (1992) Sibling cannibalism in the ladybird beetle *Harmonia axyridis*: fitness consequences for mother and offspring. *Researches in Population Ecology*, **34**, 45-55.
- Osawa, N. (1989) Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Researches in Population Ecology* **31**, 153-160.
- Park, Y.-L. et Obrycki, J.J. (2004) Spatio-temporal distribution of corn leaf Aphids (Homoptera: Aphididae) and ladybeetles (Coleoptera: Coccinellidae) in Iowa cornfields. *Biological Control*, **31**, 210-217.
- Persson, L. (1985) Asymmetrical competition: are larger animals competitively superior? *American Naturalist*, **126**, 261-266.
- Persson, L. et De Roos, A.M. (2003) Adaptive habitat use in size-structured populations: linking individual behavior to population processes. *Ecology*, **84**, 1129-1139.
- Pervez, A. et Omkar (2006) Ecology and biological control application of multicoloured Asian ladybird, *Harmonia axyridis*: A review. *Biocontrol Science and Technology*, **16**, 111-128.
- Petren, K. et Case, T.J. (1996) An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology*, **77**, 118-132.
- Petren, K. et Case, T.J. (1998) Habitat structure determines competition intensity and invasion success in Gecko lizards. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 11739-11744.
- Phoofolo, M.W. et Obrycki, J.J. (1998) Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. *Entomologia Experimentalis et Applicata*, **89**, 47-55.
- Phoofolo, M.W. et Obrycki, J.J. (1995) Comparative life-history studies of Nearctic and Palearctic populations of *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Environmental Entomology*, **24**, 581-587.

- Pickering, G., Lin, J., Riesen, R., Reynolds, A., Brindle, I. et Soleas, G. (2004) Influence of *Harmonia axyridis* on the sensory properties of white and red wine. *American Journal of Enology and Viticulture*, **55**, 153-159.
- Pimentel, D., Zuniga, R. et Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273-288.
- Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. et Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment*, **84**, 1-20.
- Pimentel, D., Lach, L., Zuniga, R. et Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience*, **50**, 53-65.
- Pimentel, D., Glenister, C., Fast, S. et Gallahan, D. (1984) Environmental risks of biological pest controls. *Oikos*, **42**, 283-290.
- Polis, G.A. (1981) The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics*, **12**, 225-251.
- Polis, G.A. (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, **138**, 123-155.
- Polis, G.A. et Holt, R.D. (1992) Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution*, **7**, 151-154.
- Polis, G.A., Myers, C.A. et Holt, R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, **20**, 297-330.
- Porter, S.D. et Savignano, D.A. (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology*, **71**, 2095-2106.
- Provost, C., Coderre, D., Lucas, É. et Bostanian, N.J. (2003) Impact of lambda-cyhalothrin on intraguild predation among three mite predators. *Environmental Entomology*, **32**, 256-263.
- Reitz, S.R. et Trumble, J.T. (2002) Competitive displacement among insects and arachnids. *Annual Review of Entomology*, **47**, 435-465.
- Revilla, T. (2002) Effects of intraguild predation on resource competition. *Journal of Theoretical Biology*, **214**, 49-62.
- Reusch, T.B.H. (1998) Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. *Marine Ecological Progress Series*, **167**, 149-153.

- Reusch, T.B.H. et Williams, S.L. (1999) Macrophyte canopy structure and the success of an invasive marine bivalve. *Oikos* **84**, 398–416
- Ricciardi, A. (2004) Assessing species invasions as a cause of extinction. *Trends in Ecology and Evolution*, **19**, 619.
- Riddick, E.W. (2006) Influence of host gender on infection rate, density and distribution of the parasitic fungus, *Hesperomyces virescens*, on the multicoloured Asian lady beetle, *Harmonia axyridis*. *Journal of Insect Science*, **6**, available online: insectscience.org/6.42.
- Riddick, E.W., et Schaefer, P.W. (2005) Occurrence, density, and distribution of parasitic fungus *Hesperomyces virescens* (Laboulbeniales: Laboulbeniaceae) on multicoloured Asian lady beetle (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America*, **93**, 1314–1321.
- Riddick, E.W., Aldrich, J.R. et Davis, J.C. (2004) DEET repels *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) adults in laboratory bioassays. *Journal of Entomological Science*, **39**, 373–386.
- Riddick, E.W., Aldrich, J.R., De Milo, A. et Davis, J.C. (2000) Potential for modifying the behavior of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) with plant-derived natural products. *Annals of the Entomological Society of America*, **93**, 1314–1321.
- Rosenheim, J.A. et Corbett, A. (2003) Omnivory and the indeterminacy of predator function: can a knowledge of foraging behavior help? *Ecology*, **84**, 2538–2548.
- Saini, E.D. (2004) Presencia de *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) en la provincia de Buenos Aires. Aspectos biológicos y morfológicos. *Ria*, **33**, 151–160.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. et Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–332.
- Sakurai, H., Kawai, T. et Takeda, S. (1992) Physiological changes related to diapause of the lady beetle, *Harmonia axydis* (Coleoptera: Coccinellidae). *Applied Entomology and Zoology*, **27**, 479–487.
- Sakurai, H., Kumada, Y. et Takeda, S. (1993) Seasonal prevalence and hibernating-diapause behavior in the lady beetle, *Harmonia axyridis*. *Researches Bulletin of the faculty of Agriculture of Gifu University*, **58**, 51–55.
- Salt, R.W. (1961) Principles of insect cold hardiness. *Annual Review of Entomology*,

6, 55-74.

- San Martin, G., Adriaens, T., Hautier, L. et Ottart, N. (2005) La coccinelle asiatique *Harmonia axyridis*. *Insectes*, **136**, 7-11.
- Sato, S., Yasuda, H. et Evans, E.W. (2005) Dropping behaviour of larvae of aphidophagous ladybirds and its effects on incidence of intraguild predation: interactions between the intraguild prey, *Adalia bipunctata* (L.) and *Coccinella septempunctata* (L.), and the intraguild predator, *Harmonia axyridis* Pallas. *Ecological Entomology*, **30**, 220-224.
- Sato, S. et Dixon, A.F.G. (2004) Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. *Agricultural and Forest Entomology*, **6**, 21-24.
- Schaefer, P.W. (2003) Winter aggregation of *Harmonia axyridis* (Coleoptera: Coccinellidae) in a concrete observation tower. *Entomological News*, **114**, 23-28.
- Schanderl, H. (1987) *Détermination des conditions optimales d'élevage de la coccinelle Harmonia axyridis Pallas (Col., Coccinellidae) et possibilité d'une production continue à l'aide d'une proie de substitution, les œufs d'Ephestia kuehniella Zeller (Lep., Pyralidae)*. Thèse de doctorat, Faculté des Sciences et Techniques de St-Jérôme, Marseille, France.
- Schanderl, L.H., Ferran, A., et Larroque, M.M. (1985) Les besoins trophiques et thermiques des larves de la coccinelle *Harmonia axyridis* Pallas. *Agronomie*, **5**, 417-422.
- Scheiner, S.M. (1993) Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, **24**, 35-68.
- Schellhorn, N.A. et Andow, D.A. (1999) Cannibalism and interspecific predation: Role of oviposition behavior. *Ecological Applications*, **9**, 418-428.
- Scherrer, B. (1984) *Biostatistique*. Gaëtan Morin. Chicoutimi, Québec, Canada.<
- Schmitz, D.C., Simberloff, D., Hofstetter, R.H., Haller, W. et Sutton, D. (1997) The ecological impact of nonindigenous plants. Pp. 39-61 in Simberloff, D., Schmitz, D.C. et Brown, T.C. (eds) *Strangers in paradise*. Island Press, Washington D.C. USA.
- Sebolt, D.C. et Landis, D.A. (2004) Arthropod predators of *Galerucella californiensis* L. (Coleoptera: Chrysomelidae): an assessment of biotic interference. *Environmental Entomology*, **33**, 356-361.
- Settle, W.H. et Wilson, L.T. (1990) Invasion by the variegated leafhopper and biotic interactions: parasitism, competition, and apparent competition. *Ecology*, **71**, 1461-1470.

- Shapiro-Illan, D.I. et Cottrell, T.E. (2005) Susceptibility of lady beetles (Coleoptera: Coccinellidae) to entomopathogenic nematodes. *Journal of Invertebrate Pathology*, **89**, 150-156.
- Shea, K. et Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170-176.
- Shea, K., Kelly, d., Sheppard, A.W. et Woodburn, T.L. (2005) Context-dependent biological control of an invasive thistle. *Ecology*, **86**, 3174-3181.
- Simberloff, D. (2005) The politics of assessing risk for biological invasions: the USA as a case study. *Trends in Ecology and Evolution*, **20**, 216-222.
- Simberloff, D., Parker, I.M. et Windle, P.N. (2005) Introduced species policy, management, and future research needs. *Frontiers of Ecology and Environment*, **3**, 12-20.
- Simberloff, D. et Stiling, P. (1996) How risky is biological control? *Ecology*, **77**, 1965-1974.
- Snyder, W.E., Clevenger, G.M. et Eigenbrode, S.D. (2004) Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia*, **140**, 559-565.
- Snyder, W.E., Joseph, S.B., Preziosi, R.F. et Moore, A.J. (2000) Nutritional benefits of cannibalism for the lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. *Environmental Entomology*, **29**, 1173-1179.
- Soares, A.O.C.M. (2000) *Importância do polimorfismo na biologia de Harmonia axyridis Pallas (Coleoptera: Coccinellidae)*. Thèse de doctorat, Universidade dos Açores, Ponta Delgada, Azores, Portugal.
- Soares, A. O. et Serpa, A. (2007) Interference competition between ladybird beetle adults (Coleoptera: Coccinellidae): effects on growth and reproductive capacity. *Population Ecology*, **49**, 37-43.
- Soares, A.O., Coderre, D. et Schanderl, H. (2001) Fitness of two phenotypes of *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.*, **98**, 287-293.
- Sokal, R.R. et Rohlf, F.J. (1995) *Biometry: the principles and practice of statistics in biological research. 3rd Edition*. W. H. Freeman, San Francisco.
- Sol, D. et Lefebvre, L. (2000) Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, **90**, 599-605.
- Sol, D., Timmermans, S. et Lefebvre, L. (2002) Behavioural flexibility and invasion success in birds. *Animal Behaviour*, **63**, 495-502.
- Somme, L. (1982) Supercooling and winter survival in terrestrial arthropods.

- Comparative Biochemistry and Physiology, A: Comparative Physiology*, **73A**, 519-543.
- Soula, B. and Menu, F. (2003) Variability in diapause duration in the chestnut weevil : mixed ESS, genetic polymorphism or bet-hedging? *Oikos*, **100**, 574-580.
- Spiller, D.A. et Schoener, T.W. (1994) Effects of top and intermediate predators in a terrestrial food web. *Ecology* **75**, 182-196.
- Stachowicz, J.J., Fried, H., Osman, R.W. et Whitlatch, R.B. (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology*, **83**, 2575-2590.
- Stewart, L.A., Hemptinne, J.-L. et Dixon, A.F.G. (1991) Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Functional Ecology*, **5**, 380-385.
- Stockwell, C.A., Hendry, A.P. et Kinnison, M.T. (2003) Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*, **18**, 94-101.
- Tauber, M.J., Tauber, C.A. et Masaki, S. (1986). *Seasonal adaptations of insects*. Oxford University Press, New York.
- Tedders, W.L. et Schaefer, P.W. (1994) Release and establishment of *Harmonia axyridis* (Coleoptera, Coccinellidae) in the southeastern United-States. *Entomological News*, **105**, 228-243.
- Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455-1474.
- Tilman, D. (1997) Community invisibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81-92.
- Turnbull, A.L. et Chant, D.A. (1961) The practice and theory of biological control of insects in Canada. *Canadian Journal of Zoology*, **39**, 697-753.
- Turnock, W.J., Wise, I.L. et Matheson, F.O. (2003) Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. *Canadian Entomology*, **135**, 391-404.
- Vermeij, G.J. (1996) An agenda for invasion biology. *Biological Conservation*, **78**, 3-9.
- Verschoor, A.M., Vos, M. et van der Stap, I. (2004) Inducible defences prevent strong population fluctuations in bi- and tritrophic food chains. *Ecology Letters*, **7**, 1143-1148.
- Vitousek, P.M., Dantonio, C.M., Loope, L.L. et Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist*, **84**, 468-478.

- Von Holle, B. (2005) Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. *Journal of Ecology*, **93**, 16-26.
- Von Holle, B. et Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212-3218.
- Vos, M., Kooi, B.W., DeAngelis, D.L. et Mooij, W.M. (2004) Inducible defences and the paradox of enrichment. *Oikos*, **105**, 471-480.
- Waage, J. (1990) Ecological theory and the selection of biological control. Dans Mackauer, J.M., Ehler, L.E. et Roland, J. (Eds) *Critical issues in biological control*. Intercept Ltd, Andover, pp. 135-158.
- Warren, L.O. et Tadic, M. (1967) Biological observations on *Coleomegilla maculata* and its role as a predator of the fall webworm. *Journal of Economic Entomology*, **60**, 1492-1496.
- Watanabe, M. (2002) Cold tolerance and myo-inositol accumulation in overwintering adults of a lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **99**, 5-9.
- Welden, C.W. et Slausen, W.L. (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *Quarterly Review of Biology*, **61**, 23-44.
- West-Eberhard, M.J. (1989) Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, **20**, 249-278.
- Wheeler, A.G. et Hoebeke, E.R. (1995) *Coccinella novemnotata* in northeastern North America: Historical occurrence and current status (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, **97**, 701-716.
- Williamson, M. (1996) *Biological Invasions*. Chapman et Hall.
- With, K.A., Pavuk, D.M., Worchuck, J.L., Oates, R.K. et Fisher, J.L. (2002) Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications*, **12**, 52-65.
- Wise, I.L., Turnock, W.J. et Roughley, R.E. (2001) New records of Coccinellid species for the province of Manitoba. *Proceedings of the Entomological Society of Manitoba*, **57**, 5-10.
- Woodward, G. et Hildrew, A.G. (2001) Invasion of a stream food web by a new top predator. *Journal of Animal Ecology*, **70**, 273-288.
- Work, T.T., McCullough, D.G., Cavey, J.F. et Komsa, R. (2005) Arrival rate of nonindigenous insect species into the United States through foreign trade.

Biological Invasions, **7**, 323-332.

- Wright, E.J. et Laing, J.E. (1982) Stage-specific mortality of *Coleomegilla maculata lengi* Timberlake on corn in southern Ontario. *Environmental Entomology*, **11**, 32-37.
- Yarbrough, J.A., Armstrong, J.L., Blumberg, M.Z., Phillips, A.E., McGahee, E. et Dolen, W.K. (1999) Allergic rhinoconjunctivitis caused by *Harmonia axyridis* (Asian lady beetle, Japanese lady beetle, or lady bug). *The Journal of Allergy and Clinical Immunology*, **104**, 704-705.
- Yasuda, H., Evans, E.W., Kajita, Y., Urakawa, K. et Takizawa, T. (2004) Asymmetric larval interactions between introduced and indigenous ladybirds in North America. *Oecologia*, **141**, 722-731.
- Yasuda, H., Kikuchi, T., Kindlmann, P. et Sato, S. (2001) Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior*, **14**, 373-384.
- Yasuda, H. et Kimura, T. (2001) Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. *Entomologia Experimentalis et Applicata*, **98**, 17-25.
- Yasuda, H. et Ohnuma, N. (1999) Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia Experimentalis et Applicata*, **93**, 63-67.
- Yasuda, H. et Shinya, K. (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga*, **42**: 153-163.
- Zitzman, A.J. et May, M.L. (1989) Growth, food consumption, and nitrogen and lipid composition of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Coccinellidae), as a function of the nitrogen supply of its host plant. *Journal of Entomological Science*, **24**, 62-69.

ANNEXE A

**ARE ANNUAL CROPS MORE PRONE TO INVASIVE SPECIES
THAN PERENNIAL CROPS ? THE CASE OF THE
MULTICOLORED ASIAN LADYBEETLE, *HARMONIA*
AXYRIDIS (COLEOPTERA: COCCINELLIDAE)**

ABSTRACT

The complexity of trophic interactions in ecosystems colonized by an invasive species is considered as one of the main factors determining its resilience to invasions. The multicolored Asian ladybeetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), was first mentioned in southern Canada in 1994. In this study, we examined the status of the ladybeetle in Quebec agroecosystems seven to ten years after its arrival. We then verified the hypothesis that success of invasive species is higher in annual than in perennial crops. We integrated the findings from eight field studies carried out in a pome fruit, a grape crop, medicinal crops, field corn, sweet corn, sweet pepper, lettuce, and soybean. Multicolored Asian ladybeetle was present in all crops, and was a dominant species of the coccinellid assemblage. This confirmed our hypothesis as the relative proportion of *H. axyridis* and invasive species in the coccinellid assemblage was higher in annual than in perennial crops.

Key-words: Coccinellidae, exotic species, invasion, multicolored Asian ladybeetle, *Harmonia axyridis*, agroecosystems, vineyard, apple, corn, sweet pepper, lettuce, annual plant, perennial plant, community resistance.

INTRODUCTION

Biological invasions usually occur in three successive stages, 1) transport of the invader to the target area, 2) establishment and growth of invasive populations, and 3) dispersion of the invader into adjacent areas (Shea and Chesson 2002). The complexity of trophic interactions in the recipient ecosystem is one of the main opposition factors of the ecosystem to the invasion. This is because it is more difficult to get established in a complex food web than in a simpler one (Hewitt and Huxel 2002; Stachowicz *et al.* 2002; Shea and Chesson 2002). Based on the availability of plant resources and the limited number of trophic links, agro-ecosystems are highly susceptible targets for biological invasions. In 1994, the multicolored Asian ladybeetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), was first recorded in Canada by Coderre *et al.* (1995). It is a palearctic species that had been introduced in Hawaii and California in 1916, 1964 and 1965 and East of the Mississippi (USA) in 1978 and 1982 (Gordon 1985; Tedders and Schaefer 1994). It is now well established throughout North America (Chapin and Brou 1991; Colunga-Garcia and Gage 1998; Gordon and Vandenberg 1991; Tedders and Schaefer 1994). *Harmonia axyridis* is an aphidophagous coccinellid that shows highly polyphagous habits (Iablokoff-Khnzorian 1982; LaMana and Miller 1996; Lucas *et al.* 1997, 1998, 2004; Koch 2003). In the USA, *H. axyridis* has established itself on numerous crops (Bacon, pers. comm.; Brown 2003; Colunga-Garcia and Gage 1998; LaMana and Miller 1996; Michaud 2002; Musser and Shelton 2003; Snyder *et al.* 2004). In Quebec, Canada, this coccinellid has been collected regularly in the St-Lawrence basin and is now encountered further North around St-Jean Lake (48°25' N, 71°5' W) and in the Abitibi region (48°30' N, 77°47' W) (Laplante pers. comm.). This eurytopic species is found in different agro-ecosystems such as forests, swamps and even urban areas (Koch 2003; Lucas unpublished). However, 10 years after its arrival, no quantitative data had been documented on its status in agroecosystems.

Harmonia axyridis is thought to affect indigenous ladybeetle species either by exploitative competition or by intraguild predation (Dixon 2000; Hironori and Katsuhiko

1997; Snyder *et al.* 2004; Yasuda and Ohnuma 1999; Yasuda *et al.* 2001; Kajita *et al.* 2000; Michaud 2002). Its establishment was followed by important decreases in natural populations of several local ladybeetle species such as *Brachiacantha ursina* (Fabricius), *Cycloneda munda* (Say) and *Chilocorus stigma* (Say) (Colunga-Garcia and Gage 1998). Adults overwinter in large numbers in human habitations. This peculiar overwintering habit has also made it a nuisance in residential areas (Kidd and Nalepa 1995; LaMana and Miller 1996; Nalepa *et al.* 1996; Yarbrough *et al.* 1999).

This study examines the abundance of the multicolored Asian ladybeetle in Quebec agroecosystems seven to ten years after its arrival and tests the hypothesis that the success of this invasive species should be higher in annual than in perennial crops.

MATERIALS AND METHODS

Pome fruit

The study was carried out in 1999 and 2000 in an organic apple orchard (planted in 1986) in Henryville (45°8' N, 73°11' W), Quebec, Canada. In both years, adult coccinellid populations were assessed from May to August by white sticky traps and by tapping apple trees on the third and sixth peripheral rows of the orchard. Tapping was done weekly over 20 apple trees over a 1 m² cloth. For each tree, eight branches were tapped three times. Branches were selected in the four cardinal points at 50 cm and 150 cm from the ground. Ten white sticky traps were also placed at these two distances from the ground on apple trees. Once a week, traps were observed and coccinellid species identified.

Grapes

The study was carried out from 2000 to 2002 in two commercial vineyards (both of 0.7 ha and planted in 1983-84) in southern Quebec, Canada. The L'Orpailleur vineyard was located in Dunham (45°07' N, 72°51' W) and it comprised only vines of the cultivar White Seyval. The Dietrich Joos vineyard was located in Iberville (45°16' N, 73°11' W), and it comprised of De Chaunac, Cayuga White and White Seyval cultivars. A two-liter

plastic container was held below a berry cluster and the cluster was tapped twice. Coccinellids fallen into the container were identified, counted, and then released in the vineyard. Each week from June to mid-September, 100 grapevines (50 'De Chaunac' and 50 'Cayuga White') were sampled at random at the Dietrich Jooss vineyard and 100 'White Seyval' grapevines were sampled at random at L'Orpailleur. Coccinellid adults were sorted out in the laboratory, identified and tallied. Voucher specimens were deposited at the Eastern Cereal and Oilseeds Research Centre, Agriculture and Agri-Food Canada, Ottawa, Canada. Except for fungicides, no insecticides were used in the plot where coccinellids were collected (Bostanian *et al.* 2003).

Medicinal crops

From the end of May to mid-September 2003, four medicinal crops, *Achillea millefolium* Linnaeus, *Valeriana officinalis* Linnaeus, *Hypericum perforatum* Linnaeus and *Echinacea purpurea* (Linnaeus) Moench, located at L'Assomption (45°50' N, 73°25' W), Quebec, Canada, were sampled weekly. The crops had been planted in 2002. Each field was divided in 36 sections, 5 m apart of each other and of other plants. In each section, two plants were examined visually each week for coccinellid eggs, larvae and adults.

Sweet Corn

During the summer 2000 and 2001, a corn field of the D'Artagnan cultivar was sampled from the beginning of July to the end of August. The field was located in Saint-Hyacinthe (45°37' N, 72°57' W), Quebec, Canada. It was divided into eight sections with 10 sampling stations in each section. Visual observations of coccinellids were done weekly on five plants, near the 10 sampling stations. Adults, larvae and eggs of coccinellids were identified and counted.

Field Corn

The study was done in three commercial corn fields in Farnham and l'Ange-Gardien (45°24' N, 72°44' W), Quebec, Canada, in 2002 and 2003. During the summer,

the fields were sampled seven times from the beginning of August to mid-October. In the center of each field, 30 plants were randomly selected and inspected for the presence and abundance of aphids and coccinellids. Eggs and early instars of coccinellids were brought to the laboratory and reared to the adult stage in an incubator (25°C, 65% R.H. and 16 Light : 8 Darkness) to be identified to the species.

Sweet pepper

The study was done in a field located in Laval (45°30' N, 73°32' W), Quebec, Canada. It was sampled two times per week from early July to mid-August 2002. Each sample consisted of 50 plants randomly selected and visually inspected. The presence and abundance of aphids and coccinellids were recorded.

Lettuce

From mid-May to mid-September 2002, 25 fields of head lettuce, romaine and leaf lettuce were sampled. The fields were located in Sherrington (45°10' N, 73°31' W), Quebec, Canada. Each two weeks, five samples per 0.4 ha were randomly selected and visually examined for coccinellid abundance.

Soybean

The study was carried out in 10 soybean fields in two agricultural areas near Quebec City (from 45°11' N to 46°44' N, from 70°57' W to 74°23' W), Quebec, Canada, between June and August 2002 and 2003. Samples were collected every two weeks by one to two hauls of sweep net in 10 zones in each field on the upper vegetation. Insects collected were brought to the laboratory for identification. Only adult coccinellids were identified.

Statistics

Among the eight crops considered, pome fruit, grapes and medicinal crops are perennial, whereas sweet corn, field corn, sweet pepper, lettuce and soybean are annual crops. In all crops where more than one year of data were available, a contingency Table

(G test) compared the relative proportions of the different species of coccinellids among the different years (SAS Institute 1996). When required, subsequent two-group G-tests were carried out. The proportion of invasive and indigenous species was also analyzed by a contingency table. Finally, the mean proportion of *H. axyridis* in the assemblage of coccinellids for the last year of data was compared in perennial and annual crops by using a one-way ANOVA. Similarly, the mean proportion of invasive species was compared by ANOVA.

RESULTS

Pome fruit

A total of 691 coccinellid specimens from 12 species of Coccinellidae were collected in 1999 (n=574) and 2000 (n=117) (Table 1). Six species were common to both years: *Propylea quatuordecimpunctata* (Linnaeus), *Coccinella septempunctata* Linnaeus, *H. axyridis*, *Coleomegilla maculata lengi* Timberlake and *Brachyacantha ursina* (Fabricius). They accounted for at least 20% of all captures. The relative proportion of the different species in the coccinellid assemblage significantly changed from 1999 to 2000 ($G_{4,682}=120.2$; $P<0.0001$) (Figure 1). In 1999 *H. axyridis* represented the largest proportion with 64% of the assemblage, but this proportion decreased to 12% in 2000. *Coleomegilla maculata lengi* constituted 8% of the assemblage in 1999, and it was the most common species in 2000 (30%). Many coccidophagous species were also sampled in this orchard in 1999 and 2000. *Brachyacantha ursina* was one of the most prevalent species with 15 and 22% of total specimens in 1999 and 2000 respectively. The proportion of introduced coccinellids (*P. quatuordecimpunctata*, *C. septempunctata*, *H. axyridis*) was 74.5% in 1999 and 33% in 2000, a significant decrease ($G_{1,688}=76.1$; $P<0.0001$).

Grapes

From 2000 to 2001, seven coccinellid species representing 88 specimens were collected from grapes (Table 1). No difference was observed in the relative proportion of the different species among the three years ($G_{8,76}=13.0$; $P=0.112$). *Coleomegilla maculata lengi* was the prevalent aphidophagous species accounting for 58, 39 and 47% of specimens respectively in 2000, 2001 and 2002 (Figure 1). The second most abundant species was *H. axyridis* with 17, 39

Table 1. Presence or absence and richness of coccinellid species in Quebec perennial and annual crops.

Coccinellid species	Pome fruit	Grape	Perennial crops				Annual crops				
			<i>Achillea millefolium</i>	<i>Echinacea purpurea</i>	<i>Hypericum perforatum</i>	<i>Valeriana officinalis</i>	Sweet corn	Field corn	Sweet pepper	Lettuce	Soybean
Aphidophagous											
<i>Propylea quatuordecimpunctata</i> L.	+	+	+	+	-	+	+	+	+	+	+
<i>Coccinella septempunctata</i> L.	+	+	+	+	+	+	+	-	+	+	+
<i>Coleomegilla maculata lengi</i> Timberlake	+	+	+	+	+	+	+	+	+	+	+
<i>Harmonia axyridis</i> Pallas	+	+	+	+	+	+	+	+	+	+	+
<i>Adalia bipunctata</i> L.	+	-	-	-	-	-	+	-	-	-	-
<i>Coccinella trifasciata perplexa</i> Mulsant	-	+	-	-	-	-	-	-	-	-	-
<i>Hippodamia parenthesis</i> Say	+	+	-	-	-	-	-	-	-	-	+
<i>Hippodamia convergens</i> Guérin	-	+	+	+	+	+	-	-	-	-	-
<i>Hippodamia variegata</i> Goeze	-	+	-	-	-	-	-	-	-	-	+
Coccidophagous											
<i>Brachyacantha ursina</i> Fabricius	+	-	-	-	-	-	-	-	-	-	+
<i>Psyllobora vigintimaculata</i> Say	+	+	-	-	-	-	-	-	-	-	-
<i>Hyperaspis binotata</i> Say	+	-	-	-	-	-	-	-	-	-	-
<i>Hyperaspis undulata</i> Say	+	-	-	-	-	-	-	-	-	-	-
<i>Chilocorus stigma</i> Say	+	-	-	-	-	-	-	-	-	-	-
<i>Nephus flavifrons</i> Melsh.	+	-	-	-	-	-	-	-	-	-	-
Richness	12	9	5	5	4	5	5	3	4	4	7

+: (+) presence of the coccinellid species. (-)

1: (+) presence of the coccinellid species, (-) absence.

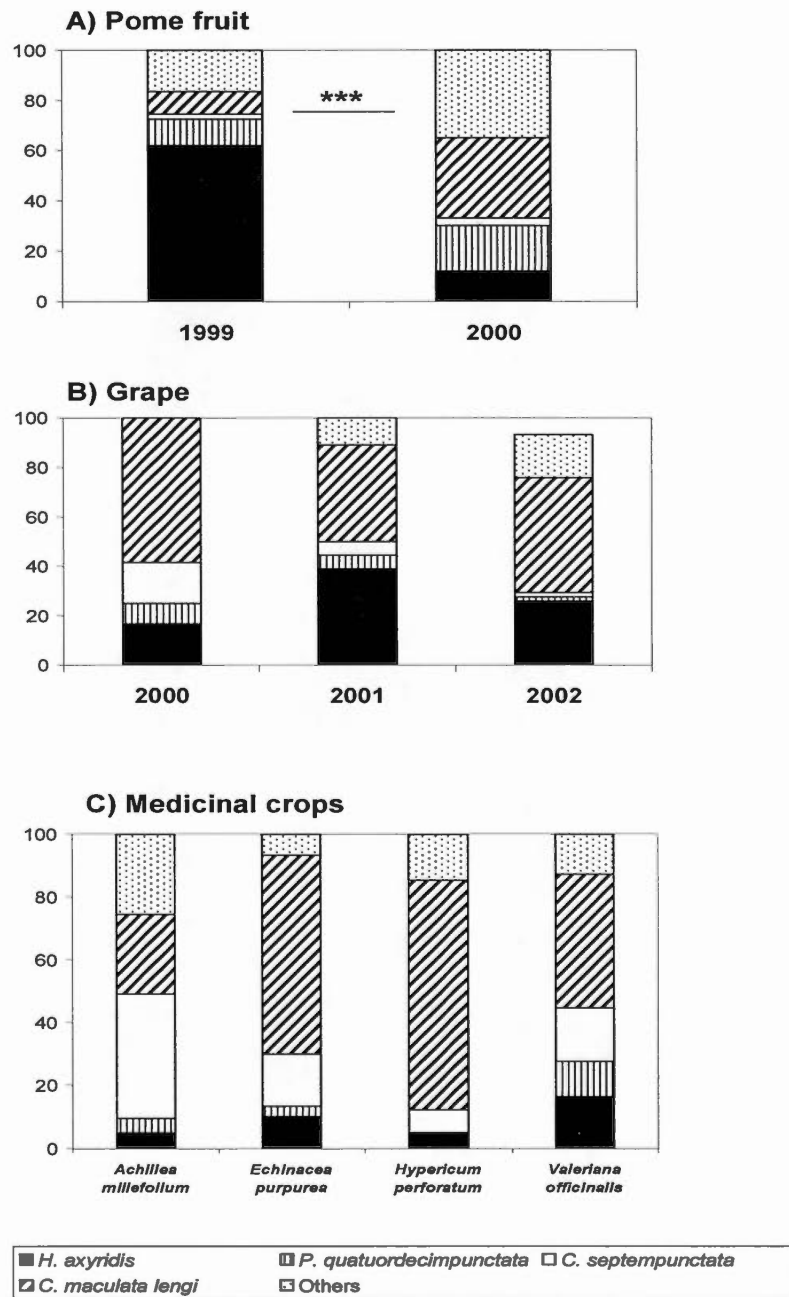


Figure 1. Proportion of coccinellid species observed in Quebec perennial crops between 1999 and 2003. Note: * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

and 26% of the captures (Figure 1). The percentage of introduced coccinellids represented 42% in 2000, 51% in 2001 and 30% in 2002 ($G_{2,85}=2.8$; $P=0.250$).

Medicinal crops

In *A. millefolium*, *C. septempunctata* comprised 39.6% of the specimens, *C. maculata lengi*, and *Hippodamia convergens* Guérin-Ménéville, were each 25.4%. Whereas, *H. axyridis*, and *P. quatuordecimpunctata*, were each 4.8% for a total of 63 coccinellids recorded. On *E. purpurea*, 141 coccinellids were observed, among which 63.3% were *C. maculata lengi*, 16.7% were *C. septempunctata*, 10.0% were *H. axyridis*, 6.7% were *H. convergens*, and 3.3% were *P. quatuordecimpunctata*. On *H. perforatum*, 41 coccinellids were collected, represented by 73.2% *C. maculata*, 7.3% *C. septempunctata*, 4.9% *H. axyridis*, and 14.6% *H. convergens*. On *V. officinalis*, 60 coccinellids were recorded during the summer, with 42.6% *C. maculata*, 17% *C. septempunctata*, 16.3% *H. axyridis*, 12.8% *H. convergens*, and 11.3% *P. quatuordecimpunctata* (Fig. 1). The percentage of introduced coccinellids on *A. millefolium*, *E. purpurea*, *H. perforatum* and *V. officinalis* represented 49.1, 30.0, 12.2 and 44.6% respectively.

Sweet corn

In 2000, 1958 specimens from five species were recorded. The coccinellid assemblage was mainly composed of 54.6% *C. maculata*, 23.4% of *P. quatuordecimpunctata*, 11.7% of *C. septempunctata*, 8.8% of *H. axyridis* and 1.5% of *Adalia bipunctata* (Linnaeus) (Figure 2). In 2001, the composition of the assemblage changed, with 4778 specimens belonging to four species ($G_{4,6728}=1204.15$; $P<0.001$). *Harmonia axyridis* was the most common species with 49.2% of the coccinellids followed by *C. maculata* (29.3%), *P. quatuordecimpunctata* (11.6%) and *C. septempunctata* (9.9%). The percentage of introduced coccinellids significantly increased from 43.9% in 2000 to 70.7% in 2001 ($G_{1,6734}=419.9$; $P<0.001$).

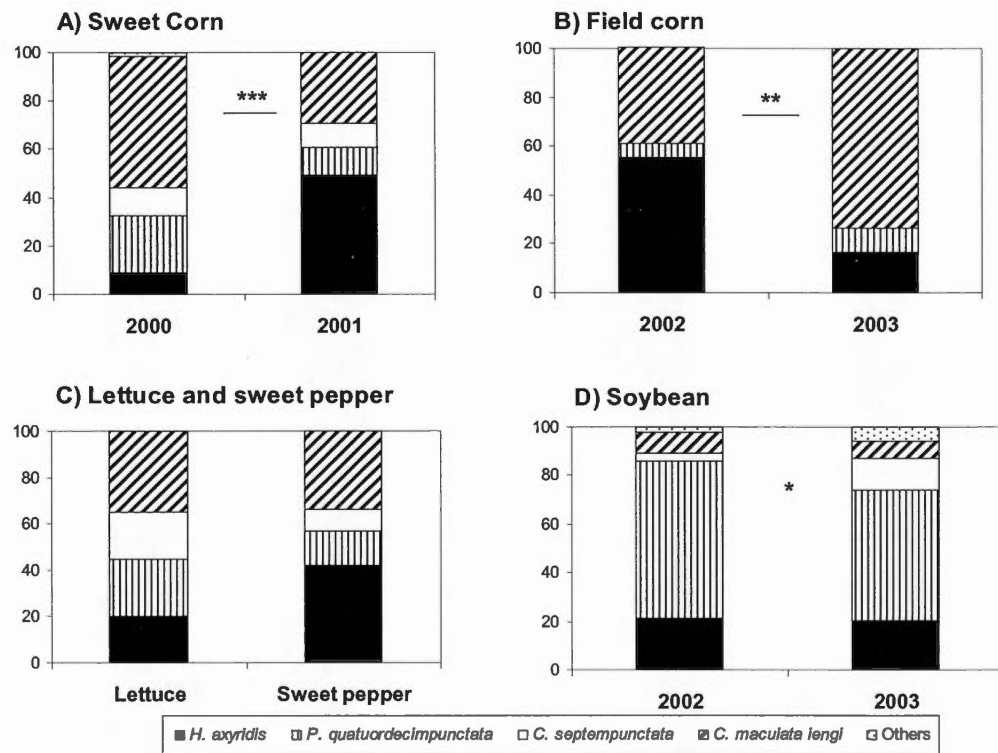


Figure 2. Proportion of coccinellid species observed in Quebec annual crops between 2000 and 2003. Note: * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Field Corn

In 2002, 1053 specimens were collected during the summer. *Propylea quatuordecimpunctata*, represented 5.7%, *C. maculata* represented 39.3% and *H. axyridis* 55.4% of the samples (Figure 2). In 2003, a total of 681 specimens of the same three species were recorded. The relative proportion of the species significantly changed from 2002 with 9.7% for *P. quatuordecimpunctata*, 73.6% for *C. maculata* and 16.7% for *H. axyridis* ($G_{2,1730}=271.68$; $P<0.001$). The percentage of introduced coccinellids changed from 61.1% in 2002 to 26.4% in 2003 ($G_{1,1732}=202.80$; $P<0.001$).

Sweet pepper

During July and August 2002, 109 adult coccinellids from four different species were collected on more than 1800 plants; *C. maculata* represented 34% of the samples, *H. axyridis* 42.2%, *P. quatuordecimpunctata* 14.7% and *C. septempunctata* 9.1% (Figure 2). No sampling was carried out in September because the grower applied pesticides following an aphid outbreak. The percentage of introduced coccinellids was 66.1%.

Lettuce

In 2002, 180 individuals from four species were collected. *Harmonia axyridis* represented 20% of the assemblage, *P. quatuordecimpunctata* 25%, *C. septempunctata* 20% and *C. maculata* 35% (Figure 2). Adults and larvae of the species were observed during the sampling. The percentage of introduced coccinellids represented 65%.

Soybean

In 2002, 265 specimens from six coccinellid species were identified: 65% were *P. quatuordecimpunctata*, 3% were *C. septempunctata*, 21.1% were *H. axyridis* and 9% were *C. maculata*. In 2003, a total of 69 specimens (seven species) of coccinellids were identified (Figure 2). The relative proportion of the different species changed with 53.6% for *P. quatuordecimpunctata*, 13% for *C. septempunctata*, 20.3% for *H. axyridis* and 7.3% for *C. maculata* ($G_{4,326}=12.5$; $P=0.014$). The percentage of introduced coccinellids

was 89.1% in 2002 and 87% in 2003 ($G_{1,359}=0.17$; $P=0.683$).

Annual vs. perennial crops

The percentage of *H. axyridis* in the coccinellid assemblage in the annual crops was significantly higher than in the perennial crops ($F_{1,10}=6.8$; $P=0.028$) (Figure 3). Moreover, invasive coccinellid species represented a greater proportion of the assemblage in annual than in perennial crops ($F_{1,10}=7.4$; $P=0.023$).

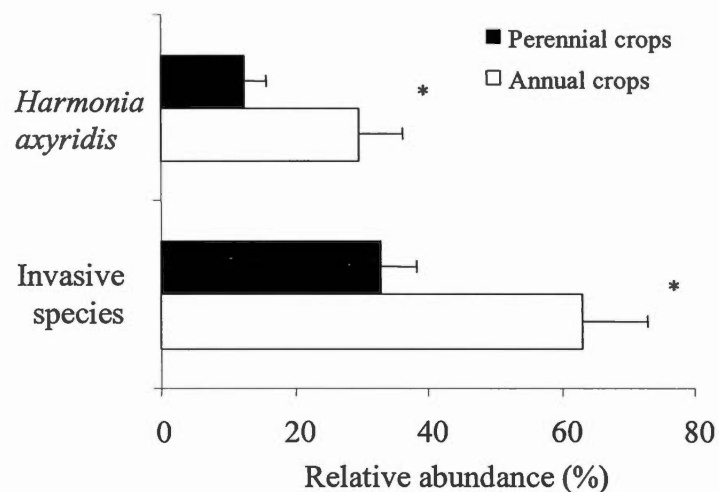


Figure 3. Relative proportion of the abundance of *H. axyridis* and the invasive species (*H. axyridis*, *P. quatuordecimpunctata* and *C. septempunctata*) in the coccinellid assemblage. Note: * indicate $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

DISCUSSION

The results of this study indicate that seven to ten years after its arrival, *H. axyridis* is one of the dominant coccinellid species in most crops of Eastern Canada. Other unpublished data from the same area indicated that this coccinellid is also present in raspberry, canola, and celery. In raspberry for example, *H. axyridis* represented 1.1% of the coccinellid collected in 1995 and 18.7% in 1996 (total of 374 and 916 specimens collected in 1995 and 1996) (Roy unpublished data). In soybean, the arrival of this coccinellid coincided with the arrival of the soybean aphid, *Aphis glycines* Matsumura (Fox *et al.* 2004). The species has also been observed on aspen, birch, willow and fir. Our study reports results from several agroecosystems, where the species is well adapted. However, its eurytopic habits include forest and other natural systems (Teddars and Schaefer 1994). It has also been observed in swamp ecosystems and urban areas (e.g. Montreal, Canada). Geographically, this invader is reported throughout southern Quebec and as far North as Abitibi (48°30' N, 77°47' W). This colonization reflects a huge success for this invasive species.

The results also confirm our hypothesis that perennial crops are harder to be colonized by an invasive species than annual crops. In this respect, our results show that the relative proportion of invasive species in the coccinellid assemblage was higher in annual (67.4%) than in perennial (33.0%) crops. Furthermore, the relative proportion of *H. axyridis* in the coccinellid assemblage was higher in annual (30.2%) than in perennial (12.3%) crops.

In recent years, Quebec agro-ecosystems have been invaded by three coccinellids. These are: *P. quatuordecimpunctata* probably in the 1960s (Gordon 1985), *C. septempunctata* in 1973 (Larochelle 1979) and *H. axyridis* in 1994 (Coderre *et al.* 1995). These species actually represent at least 25% of the coccinellids encountered. These species are polyphagous predators attacking a great diversity of prey including aphids, mites, scales, lepidopteran and coleopteran larvae (Hodek and Honěk 1996). They are also eurytopic species, exploiting a great diversity of habitats. Consequently, they may

have caused considerable changes in various ecosystems. These changes may have been brought about by classical predation, exploitative competition or intraguild predation. Their main impact would be 1) on other species of the aphidophagous guild, 2) on endangered species and 3) on biological control of aphids. For example, in 1978, indigenous species represented 100% of the coccinellid assemblage in southern Quebec field corns. The coccinellids were: 74.5% of *Hippodamia tredecimpunctata tibialis* (Say) and 24.1% for *C. maculata* (Coderre unpublished data). For over five years now, *H. tredecimpunctata tibialis* has completely disappeared from the corn fields.

The success of an invasive species to colonize a given area may be affected positively or negatively by the presence of other species. For example, *Dinocampus coccinellae* Schrank is one of the most devastating parasitic braconid of coccinellids, yet the rate of *H. axyridis* parasitism by this braconid is very low. Thus, in the presence of this parasite the speed of colonization by *H. axyridis* is accelerated as most of the native coccinellids succumb to the parasite (Hoogendoorn and Heimpel 2002; Firlej *et al.* 2005). In other studies, Brown and Miller (1998) and Lucas *et al.* (2002) showed that a species may be more at risk to the invader than other species because of their habitat in the ecosystem. For example, *C. maculata lengi* is more abundant on the lower parts of plants and avoids competition with *H. axyridis*, which is found on the upper parts of plants (Musser and Shelton 2003). As a result of its habitat, *C. maculata lengi* is able to coexist with *H. axyridis* in corn fields.

The multicolored Asian ladybeetle is now well established in most crops and agroecosystems in Canada and USA. The consequences of such an invasion may also affect adversely other natural enemies of aphids such hover flies, lacewings, gall midges, hemipteran predators, by competition and intraguild predation (Horn 1991; Koch *et al.* 2003). The arrival of the multicolored Asian ladybeetle has been associated with significant changes in native guild structures (Tedders and Schaeffer 1994; Brown and Miller 1998; LaMana and Miller 1996; Reitz and Trumble 2002; Snyder *et al.* 2004; Michaud 2002). This coccinellid has demonstrated a propensity to intraguild predation on

local coccinellid species (Hironori and Katsuhiro 1997; Snyder *et al.* 2004; Yasuda and Shinya 1997; Yasuda and Ohnuma 1999; Yasuda *et al.* 2001; Kajita *et al.* 2000; Michaud 2002).

Co-existence of different species involved with an invader is difficult to assess. It requires theoretically that the native predator (intraguild prey) be superior at exploiting the prey better than the invasive predator (if this species is confirmed as a superior intraguild predator) (Holt and Polis 1997; Mylius *et al.* 2001; Diehl and Feissel 2000; Morin 1999). In most cases, the control of aphids (prey) was not altered by the arrival of *H. axyridis* (Rice *et al.* 1998; Tedders and Schaefer 1994; Brown and Miller 1998; Michaud 1999; 2000; 2002; Lucas *et al.* 2002; Hoogendorn and Heimpel 2004; Musser and Shelton 2003; Evans 2004).

In conclusion, the multicolored Asian ladybeetle is now one of the predominant coccinellids in most of agroecosystems and possibly of forest and urban systems in eastern Canada. Furthermore, perennial crops appear to have higher resilience to biological invasions than annual crops. Our results should be revisited in the context of a long term study (over 20 years after invasion).

ACKNOWLEDGEMENTS

This research was supported by NSERC scholarship for Geneviève Labrie, NSERC grant to Daniel Coderre and Eric Lucas. The authors express their gratitude to the late Victor Dietrich, Christiane Jooss and Charles-Henri de Coussergues proprietors of Dietrich-Jooss and L'Orpailleur vineyards. Benoit Rancourt, Julie Bellemare, and Martin Trudeau are also thanked for their participation in the study. Laurent Lesage confirmed the identification of specimens. The vineyard study, co-financed by Agriculture and Agri-Food Canada and Dietrich-Jooss and L'Orpailleur vineyards, was granted to Noubar J. Bostanian and Charles Vincent (MII project AAC# 97-5735). We also thank Michèle Roy, M.-L. Pelletier, S. Tremblay for unpublished data on the multicolored Asian ladybeetle.

REFERENCES

- Bostanian, N.J., Vincent, C., Goulet, H., Lesage, L., Lasnier, J., Bellemare, J. and Mauffette, Y. (2003) The arthropod fauna of Quebec vineyards with particular reference to phytophagous arthropods. *Journal of Economic Entomology*, **96**, 1221-1229.
- Brown, M.W. and Miller, S.S. (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News*, **109**, 143-151.
- Brown, M.W. (2003) Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl*, **48**, 141-153.
- Chapin, J.B. and Brou, V.A. (1991) *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, **93**, 630-635.
- Coderre, D., Lucas, E. and Gagné, I. (1995) The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) in Canada. *Canadian Entomologist*, **127**, 609-611.
- Colunga-Garcia, M. and Gage, S.H. (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology*, **27**, 1574-1580.
- Diehl, S. and Feissel, M. (2000) Effects of enrichment on three-level food chains with omnivory. *American Naturalist*, **155**, 200-218.
- Dixon, A.F.G. (2000) Insect predator-prey dynamics: ladybird beetles and biological control. Cambridge University Press, Cambridge.
- Evans, E.W. (2004) Habitat displacement of North American ladybirds by an introduced species. *Ecology*, **85**, 637-647.
- Firlej, A., Boivin, G., Lucas, E. and Coderre, D. (2005) First report of parasitism of

- Harmonia axyridis* by *Dinocampus coccinellae* Schrank in Canada. *Biological Invasions*, **7**, 553-556.
- Gordon, R.D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of New York Entomological Society*, **93**, 1-912.
- Gordon, R.D. and Vandenberg, N. (1991) Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. *Proceedings of the Entomological Society of Washington*, **93**, 845-864.
- Hewitt, C.L. and Huxel, G.R. (2002) Invasion success and community resistance in single and multiple species invasion models: do the models support the conclusions? *Biological Invasions*, **4**, 263-271.
- Hironori, Y. and Katsuhiko, S. (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga*, **42**, 153-163.
- Hodek, I. and Honěk, A. (1996) *Ecology of Coccinellidae*. The Netherlands, Kluwer Academic Publishers.
- Holt, R.D. and Polis, G.A. (1997) A theoretical framework for intraguild predation. *American Naturalist*, **149**, 745-764.
- Hoogendoorn, M. and Heimpel, G.E. (2002) Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. *Biological Control*, **25**, 224-230.
- Hoogendoorn, M. and Heimpel, G.E. (2004) Competitive interactions between an exotic and a native ladybeetle: a field cage study. *Entomologia Experimentalis et Applicata*, **111**, 19-28.
- Horn, D.J. (1991) Potential impact of *Coccinella septempunctata* on endangered Lycaenidae (Lepidoptera) in Northwestern Ohio, USQ. In Polgar, L., Chambers,

- R.J., Dixon, A.F.G. and Hodek, I. (eds): Behaviour and impact of Aphidophaga. SPB Academic Publishing bv. The Hague, The Netherlands, pp. 159-162.
- Iablokoff-Khnzorian, S.M. (1982) Les coccinelles, Coléoptères-Coccinellidae. Société Nouvelle des Éditions Boubée, Paris, 568 pp.
- Kajita, Y., Takano, F., Yasuda, H. and Agarwala, B.K. 2000: Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. *Applied Entomology and Zoology*, **35**, 473-479.
- Kidd, K. and Nalepa, C.A. (1995) Distribution of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in North Carolina and Virginia. *Proceedings of the Entomological Society of Washington*, **97**, 729-731.
- Koch, R.L. (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science*, **3**, 1-16.
- Koch, R.L., Hutchison, W.D., Venette, R.C. and Heimpel, G.E. (2003) Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biological Control*, **28**, 265-270.
- LaMana, M.L. and Miller, J.C. (1996) Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biological Control*, **6**, 232-237.
- Larochelle, A. (1979) Les Coléoptères Coccinellidae du Québec. *Cordulia*, supplément **10**, 1-111.
- Lucas, E., Coderre, D. and Vincent, C. (1997) Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. *Entomologia Experimentalis et Applicata*, **85**, 151-159.
- Lucas, E., Coderre, D. and Brodeur, J. (1998) Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology*, **79**,

1084-1092.

- Lucas, E., Gagné, I. and Coderre, D. (2002) Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **99**, 457-463.
- Lucas, E., Demougeot, S., Vincent, C. and Coderre, D. (2004) Effect of the presence of a second prey species on the voracity of *Coccinella septempunctata* and *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **101**, 37-41.
- Michaud, J.P. (1999) Sources of mortality in colonies of brown citrus aphid, *Toxoptera citricida*. *BioControl*, **44**, 347-367.
- Michaud, J.P. (2000) Development and reproduction of ladybeetles (Coleoptera: Coccinellidae) on the citrus aphids *Aphis spiraecola* Patch and *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae). *Biological Control*, **18**, 287-297.
- Michaud, J.P. (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. *Environmental Entomology*, **31**, 827-835.
- Morin, P. (1999) Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology*, **80**, 752-760.
- Musser, F.R. and Shelton, A.M. (2003) Factors altering the temporal and within-plant distribution of coccinellids in corn and their impact on potential intraguild predation. *Environmental Entomology*, **32**, 575-583.
- Mylius, S.D., Klumpers, K., De Roos, A.M. and Persson, L. (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist*, **158**, 259-276.
- Nalepa, C.A., Kidd, K.A. and Ahlstrom, K.R. (1996) Biology of *Harmonia axyridis* (Coleoptera, Coccinellidae) in winter aggregations. *Annals of the Entomological Society of America*, **89**, 681-685.

- Reitz, S.R. and Trumble, J.T. (2002) Competitive displacement among insects and arachnids. *Annual Review of Entomology*, **47**, 435-465.
- Rice, N.R., Smith, M.W., Eikenbary, R.D., Arnold, D., Tedders, W.L., Wood, B., Landgraf, B.S., Taylor, G.G. and Barlow, G.E. (1998) Assessment of legume and nonlegume ground covers on Coleoptera: Coccinellidae density for low-input pecan management. *American Journal of Alternative Agriculture*, **13**, 111-123.
- SAS Institute. (1996) "JMP In, version 3.2." SAS Institute Inc., Cary, North Carolina.
- Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends Ecology and Evolution*, **17**, 170-176.
- Snyder, W.E., Clevenger, G.M. and Eigenbrode, S.D. (2004) Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia*, **140**, 559-565.
- Stachowicz, J.J., Fried, H., Osman, R.W. and Whitlatch, R.B. (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology*, **83**, 2575-2590.
- Tedders, W.L. and Schaefer, P.W. (1994) Release and establishment of *Harmonia axyridis* (Coleoptera, Coccinellidae) in the Southeastern United-States. *Entomological News*, **105**, 228-243.
- Yarbrough, J.A., Armstrong, J.L., Blumberg, M.Z., Phillips, A.E., McGahee, E., and Dolen, W.K. (1999) Allergic rhinoconjunctivitis caused by *Harmonia axyridis* (Asian lady beetle, Japanese lady beetle or lady bug). *Journal of Allergy and Clinical Immunology*, **104**, 704-705.
- Yasuda, H. and Ohnuma, N. (1999) Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia Experimentalis et Applicata*, **93**, 63-67.
- Yasuda, H. and Shinya, K. (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga*, **42**,

153-163.

Yasuda, H., Kikuchi, T., Kindlmann, P. and Sato, S. (2001) Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior*, **14**, 373-384.

ANNEXE B

**THE MULTICOLOURED ASIAN LADY BEETLE, *HARMONIA*
AXYRIDIS - BENEFICIAL OR NUISANCE ORGANISM?**

The road to hell is paved with good intentions.

(frequently but mistakenly credited to Samuel Johnson: the original quotation should be credited to Saint Bernard of Clairvaux (1091-1153) as "Hell is full of good intentions or desires.")

Overview (100 words max): The multicoloured Asian lady beetle (MALB) is one of the most voracious and polyphagous Coccinellid predators in the world. For biocontrol purposes it has been introduced several times in North America where it is now well established. Although importation of MALB has been done primarily help agriculture, MALB caused several unexpected problems. Because of its polyphagy and aggressiveness as predator, it displaces several indigenous and imported Coccinellid species in several agro-ecosystems. In the fall, it frequently enters houses by thousands and is a serious nuisance. In vineyards adults taint the wine when grapes are pressed at harvest.

In the minds of most people, Coccinellids are friendly and beneficial insects. They are brightly coloured, ubiquitous and are predators that help farmers. When we were young we read poems and drew pictures of ladybugs while in school. Teachers used Coccinellids to illustrate us basic ecological principles. These beetles are easy to rear and they make excellent experimental subjects to test numerous hypotheses relevant to biocontrol (e.g. Hodek and Honěk 1996, Dixon 2000). In college biology courses we learned that, except for a few phytophagous species, Coccinellids are voracious predators and are major players in successful biocontrol programs. In other words, we have been taught that Coccinellids are almost perfect. But are they?

As scientists, we know that things are generally not that simple. A case in point is *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), the multicoloured Asian lady beetle (MALB) (also named the Harlequin lady beetle in England), a Coccinellid that was released in the USA for biocontrol purposes (Koch 2003, Pervez and Omkar 2006). Why did a biocontrol program, intended for the public good in agriculture,

unexpectedly turned sour, to the point where negative headlines were published in the major media of North America? This was an unusual and unfortunate situation that may have destroyed years of efforts by scientists to demonstrate the value of biological control programs to the general public.

Why did this happen? What can we learn from this experience? First, we will briefly discuss the origin, biology and releases of *H. axyridis*. Then, we will address its intended effects in agricultural systems. Unintended consequences of this beetle will be discussed from two points of views, i.e. agricultural (e.g. intraguild effects and *H. axyridis* as prey) and non-agricultural settings.

A few attributes

Among Coccinellids, the palearctic *H. axyridis* has a high potential for biocontrol. The species is one of the largest aphidophagous Coccinellids, is highly voracious, polyphagous (its diet includes aphids, pollen, Lepidopteran and Coleopteran eggs and larvae, mites, and probably any small soft-bodied insect), and eurytopic (its habitat includes marshes, forest, agricultural and urban areas) (Iablokoff-Khnzorian 1982). *H. axyridis* can be successfully reared on spoiled grapes. It is considered the most fecund species of all Coccinellids (Iablokoff-Khnzorian 1982) and adapts quite easily to different environments (Adriaens *et al.* 2003). Because of these traits, this beetle is a prime candidate for classical biocontrol programs. Incidentally, it is the Coccinellid species showing the largest diversity of color variants in the world - a scientifically puzzling feature that may bring confusion about its correct identification by laypersons.

Origin and dispersion over the years - from Eastern-Asia to world invasion

H. axyridis originates in northeastern Asia (Iablokoff-Khnzorian 1982). Japanese specimens were released several times in North America as a biological control agent, notably in California in 1916, 1964 and 1965 and in Nova Scotia, Connecticut,

Delaware, Georgia, Louisiana, Maine, Maryland, Mississippi, Ohio, Pennsylvania, and Washington from 1978 to 1982 (Gordon 1985).

The first established population was reported in Louisiana in 1988 (Chapin and Brou 1991) and it spread rapidly across North America (Coderre *et al.* 1995; Tedders and Schaefer 1994). It is now distributed from coast to coast from Florida to the 48th parallel in Quebec. The species was also recently found in South America (de Almeida and da Silva 2002).

Releases of *H. axyridis* were also conducted in the Ukraine in 1964, south-eastern Kazakhstan in 1969, in southern France in 1982, in the Azores Islands and in Greece in 1993. Observations of established populations of this species in Europe have been recently reported in Great Britain, in Southern France, in Greece, in Germany and in Belgium (Adriaens *et al.* 2003; Majerus *et al.* 2006).

***Harmonia axyridis* as a biocontrol agent- intended effects**

Upon review of 28 studies of *H. axyridis* as a biocontrol agent, it becomes clear that the Coccinellid is an effective predator of aphids (24 species), as well as other prey such as mites (Tetranychidae), Coleoptera and Lepidoptera (Table 1). The majority of studies reviewed found *H. axyridis* had potential as a biocontrol, with 4% complementary and 25% showing potential (Table 1). Other cases, representing 14% of our sample, reported negligible or no impact of the lady beetle on the targeted prey. However, our selection of studies may have overlooked the impact of *H. axyridis* on other non-targeted prey. Since non-targeted prey are rarely taken into account, the lady beetle may have effected other potential prey but without disrupting the biocontrol of the targeted pest.

***Harmonia axyridis* as a guild member**

H. axyridis belongs to many numerous ecological guilds (*sensu* Polis *et al.* 1989), most notably the aphidophagous predators. This guild is diverse and includes

ground beetles, lady beetles, hover flies, cecidomyids, brown and green lacewings, hemipteran predators, parasitoids and pathogens. The arrival of *H. axyridis* has generated tremendous changes in the guild structures and their dynamics. In a study of 8 different crops in Quebec, *H. axyridis* became the most commonly observed species of the Coccinellid assemblage in all cases, only a few years after its arrival.

The introduction of generalist entomophagous insects can have a drastic impact on native competing species (Simberloff and Stiling 1996; Kimberling 2004; van Lenteren *et al.* 2003). It appears that *H. axyridis* impacts its competitors by exploitative competition and/or by intraguild predation (Table 2). In the 24 studies on impact of *H. axyridis* on non-target species, 15 aphidophagous species, including 11 Coccinellids, were identified as intraguild prey and two others species were non-targeted insects that could be vulnerable (Table 2). *Harmonia axyridis* was also observed as eating *G. californiensis*, which is a biocontrol agent of *Lythrum salicaria* L. (Table 2). *Harmonia axyridis* is also a potential prey of other guild members with most intraguild predation occurring during the early instars. However, after the third instar, *H. axyridis* seems to be out of danger. The time of arrival of *H. axyridis* and its competitors at the aphid colony also determines the relative size of the aphidophagous organisms and consequently the occurrence, direction and symmetry of the intraguild predation between *H. axyridis* and its competitors (Lucas 2005). In summary, *H. axyridis* can have a significant impact upon guilds it belongs to. It is often the intraguild predator and rarely the intraguild prey.

***Harmonia axyridis* as a phytophagous species**

H. axyridis exploits an array of animal (zoophagous) resources, but also may exploit plant material (phytophagous) such as pollen and nectar. Recently, *H. axyridis* has been documented to feed on fruit in the autumn, mainly when they are injured (Table 3). This damage can be significant and the beetle has attained pest status in some fruit crops when populations explodes. In vineyards, grapes can be tainted by

the alkaloids that are released by the beetles when they are crushed with the grapes before the fermentation process (Ejbich 2003). Other fruit attacked in the fall include plum, raspberries and apple (Table 3).

Table 1. Efficiency of biological control by *Harmonia axyridis* on different pests species in different introduction countries.

Pest species	Plant species	Study	Biological control	Country or states	References
1 <i>Matsucoccus resinosa</i> Bean and Godwin, red pine scale	<i>Pinus resinosa</i> Ait.	Field cages, Field	potential	Connecticut, USA	McClure 1987
2 <i>Monellia caryella</i> (Fitch) blackmargined aphid	pecan orchard	Field	excellent control	Georgia, USA	Tedders and Schaefer 1994
<i>Monellopsis pecanis</i> Bissell, yellow pecan aphid	pecan orchard	Field	excellent control	Georgia, USA	
3 <i>Macrosiphum rosae</i>	roses	Field	effective	France	Ferran <i>et al.</i> 1996
4 pecan aphid complex	pecan orchard	Field	effective (IPM)	New Mexico, USA	LaRock and Ellington 1996
5 <i>Aphis gossypii</i> Glover, cotton aphid	cucumbers	Field	not effective	Suisse	Fischer and Leger 1997
6 <i>Phorodon humili</i> (Shrank), damson-hop aphid	hops	Field	effective	France	Trouve <i>et al.</i> 1997
7 <i>Aphis gossypii</i> Glover, cotton aphid	melon	Field	effective	Italy	Orlandini and Marteluci 1997
8 <i>Aphis spiraeicola</i> Pagenstecher, spirea aphid	apple orchard	Field	effective	West Virginia, USA	Brown and Miller 1998
9 pecan aphid	pecan orchard	Field	effective	southeastern USA	Rice <i>et al.</i> 1998
10 <i>Toxoptera citricida</i> , brown citrus aphid	citrus groves	Field	effective	Puerto Rico, Florida U	Michaud 1999
11 <i>Adelges tsugae</i>	hemlock tree	Field	negligible	North Carolina, VA, US	Wallace and Hain 2000
12 <i>Diaphorina citri</i> Kuwayama, Asian citrus psyllid	citrus groves	Field	potential	Florida, USA	Michaud 2002a
13 <i>Diaprepes abbreviatus</i> (L.), Root weevil (Coleoptera: Curculionidae)	citrus groves	Field	potential	Florida, USA	Stuart <i>et al.</i> 2002
14 <i>Tetranychus urticae</i> Koch, twospotted spider mite	citrus	Laboratory, greenhouse	potential	Florida, USA	Lucas <i>et al.</i> 2002
<i>Aphis citricola</i> Van der Goot, spirea aphid	apple trees	Laboratory	not effective	Québec, Canada	
15 <i>Rhopalosiphum maidis</i> , corn aphid	sweet corn	Laboratory	not effective		
16 <i>Ostrinia nubilalis</i> (Hübner) (Lepidoptera: Crambidae)	sweet corn	Field	potential	New York, USA	Musser and Shelton 2003c
17 <i>Acyrtosiphon pisum</i> (Harris), pea aphid	alfalfa	Field and Laboratory	negligible	New York, USA	Musser and Shelton 2003b
18 <i>Diaphorina citri</i> Kuwayama, Asian citrus psyllid	citrus groves	Field and Laboratory	additive	Wisconsin, USA	Snyder and Ives 2003
19 <i>Aphis glycines</i> Matsumura, soybean aphid	soybean	Field	effective	Florida, USA	Michaud 2004
20 <i>Aphis spiraeicola</i> , spirea aphid	apple orchard	Field	effective	Michigan, USA	Fox <i>et al.</i> 2004
21 <i>Macrosiphum euphorbiae</i> Thomas, potato aphid	roses	Field	effective	West Virginia, USA	Brown 2004
22 <i>Aphis gossypii</i> Glover, cotton aphid	cotton	greenhouses	complementary	Washington, USA	Snyder <i>et al.</i> 2004a
23 <i>Leptinotarsa decemlineata</i> , Colorado potato beetle (Coleoptera: Chrysomelidae)	potato	Laboratory	potential	UK	Tsaganou <i>et al.</i> 2004
24 <i>Periphraciphilus tessellatus</i> (Fitch) woolly alder aphid	<i>Ailanthus serrulata</i> (Ait.)	Laboratory	no change	Washington, USA	Snyder and Clevenger 2004
25 <i>Macrosiphum euphorbiae</i> Thomas, potato aphid	potato crops	Laboratory	preference	eastern USA	Butin <i>et al.</i> 2004
<i>Aphis nasturtii</i> Kaltenebach, buckthorn aphid		Field	effective	Northern Maine, USA	Alyokhin and Sewell 2004
<i>Myzus persicae</i> Sulzer, green peach aphid		Field	effective		
26 <i>Panonychus citri</i> (McGregor), citrus red mite	citrus	Laboratory	potential	Florida, USA	Villanueva <i>et al.</i> 2004
27 <i>Rhopalosiphum maidis</i> , corn aphid	Field corn	Field cages	effective	Québec, Canada	Labrie <i>et al.</i> unpubl. data

Note : 1- *Environmental Entomology* 16, 224-230; 2- *Entomological News* 105, 228-243; 3- *European Journal of Entomology* 93, 59-67; 4- *Southwestern Entomologist* 21, 153-166; 5- *Revue Suisse de Viticulture, Arboriculture et Horticulture* 29, 119-126; 6- *Entomophaga* 42, 57-62; 7- *Culture Protette* 6, 33-36; 8- *Entomological News* 109, 143-151; 9- *American Journal of Alternative Agriculture* 13, 111-123; 10- *BioControl* 44, 347-367; 11- *Environmental Entomology* 29, 638-644; 12- *Entomological News* 113, 216-222; 13- *Florida Entomologist* 85, 409-416; 14- *European Journal of Entomology* 99, 457-463; 15- *Journal of Economic Entomology* 96, 71-80; 16- *Environmental Entomology* 32, 1131-1138; 17- *Ecology* 84, 91-107; 18- *Biological Control* 29, 260-269; 19- *Environmental Entomology* 33, 608-618; 20- *Biological Control* 29, 189-198; 21- *Biological Control* 30, 229-235; 22- *Biological Control* 31, 138-144; 23- *Biological Control* 31, 353-361; 24- *Journal of Economic Entomology* 97, 1635-1641; 25- *Biological Invasions* 6, 463-471; 26- *Journal of Entomological Science* 39, 23-29

Table 2. Non-target impacts of *H. axyridis* on coccinellids species, other intraguild prey and other insects.

Non-target species		Plant species	Effect	Country or states	References
Coccinellids species					
1	<i>Coccinella septempunctata</i>	Apple orchard	Abundance decrease	West Virginia, USA	Brown and Miller 1998
2	<i>Coleomegilla maculata</i> DeGeer	Laboratory	IGP	Kentucky, USA	Cottrell and Yeagan 1998
3	<i>Brachiacantha ursina</i>	Agricultural landscape	Abundance decrease	Michigan, USA	Colunga-Garcia and Gage 1998
	<i>Cycloneda munda</i>		Abundance decrease		
4	<i>Adalia bipunctata</i> L.	Laboratory	IGP; possible impact in field	Japan	Kajita et al. 2000
5	<i>Adalia bipunctata</i> L.	Laboratory	IGP	Italy	Burgio et al. 2002
6	<i>Cycloneda sanguinea</i> L.	Citrus groves	Abundance decrease	Florida, USA	Michaud 2002b
7	<i>Coccinella septempunctata</i>	Apple orchard	Abundance decrease	West Virginia, USA	Brown 2003
8	<i>Adalia bipunctata</i> L.	Laboratory	Negligible impact	Italy	Santi et al. 2003
9	<i>Coleomegilla maculata</i> DeGeer	Field, Sweet corn	IGP	New York, USA	Musser and Shelton 2003a
10	<i>Coccinella transversoguttata</i> Brown	Potato crop	Abundance decrease	Maine	Alyokhin and Sewell 2004
11	<i>Adalia bipunctata</i> L.	Laboratory	Possible impact in field	Norwich, U.K.	Sato and Dixon 2004
12	<i>Coccinella transversoguttata</i> Brown	Laboratory	IGP	Washington, USA	Snyder et al. 2004b
	<i>Hippodamia convergens</i> Guérin-Ménéville	Laboratory	IGP	Washington, USA	
13	<i>Coleomegilla maculata</i> DeGeer	Laboratory	Possible impact in field	Kentucky, USA	Cottrell 2004
	<i>Olla v-nigrum</i> Mulsant	Laboratory	Possible impact in field	Kentucky, USA	
14	<i>Coleomegilla maculata</i> lengi Timberlake	Field cage, Corn	Abundance decrease, High resource	Québec, Canada	Labrie et al. unpublished data
15	<i>Coleomegilla maculata</i> lengi Timberlake	Laboratory	IGP	Québec, Canada	Labrie et al. unpublished data
	<i>Propylea quatuordecimpunctata</i> L.	Laboratory	IGP	Québec, Canada	
16	<i>Coccinella undecimpunctata</i> L.	Laboratory	IGP	Azores, Portugal	Félix and Soares 2004
17	<i>Coccinella transversoguttata</i> Brown	Laboratory	IGP	Utah, USA	Yasuda et al. 2004
	<i>Hippodamia convergens</i> Guérin-Ménéville	Laboratory	IGP	Utah, USA	
18	<i>Coleomegilla maculata</i> DeGeer	Laboratory	IGP	Georgia, USA	Cottrell 2005
	<i>Olla v-nigrum</i> Mulsant	Laboratory	IGP		
Other intraguild prey					
19	<i>Chrysoperla carnea</i> Stephens (Neuroptera: Chrysopidae)	Laboratory	IGP	Iowa, USA	Phoofolo and Obyrcki 1998
20	<i>Aphidoletes aphidimyza</i> Rondani (Diptera: Cecidomyiidae)	Field	Abundance decrease	West Virginia, USA	Brown 1999
21	<i>Aphidius ervi</i> Haliday (Hymenoptera: Braconidae)	Field and laboratory, Alfalfa	IGP	Wisconsin, USA	Snyder and Ives 2003
22	<i>Tamania radiata</i> (Waterston) (Hymenoptera: Eulophidae)	Citrus groves	IGP	Florida, USA	Michaud 2004
Other insects					
23	<i>Danaus plexippus</i> L. (Lepidoptera: Nymphalidae)	Laboratory and field cages	Abundance decrease	Minnesota, USA	Koch et al. 2003; Koch et al. 2005
24	<i>Galerucella calmanensis</i> L. (Coleoptera: Chrysomelidae)	<i>Lythrum salicaria</i> , Field and laboratory	Predation; Potential of disruption of biocontrol of <i>Lythrum salicaria</i>	Michigan, USA	Sebolt and Landis 2004

Note: 1- *Entomological News* 109, 143-151; 2- *Journal of Kansas Entomological Society* 71, 159-163; 3- *Environmental Entomology* 27, 1574-1580; 4- *Applied Entomology and Zoology* 35, 473-479; 5- *Biological Control* 24, 110-116; 6- *Environmental Entomology* 31, 827-835; 7- *BioControl* 48, 141-153; 8- *Bulletin of Insectology* 56, 207-210; 9- *Environmental Entomology* 32, 575-585; 10- *Biological Invasions* 6, 463-471; 11- *Agricultural and Forest Entomology* 6, 21-24; 12- *Oecologia* 140, 559-565; 13- *Biological Control* 31, 362-371; 16- *European Journal of Entomology* 101, 237-242; 17- *Oecologia* 141, 722-731; 18- *Biological Control* 34, 159-164; 19- *Entomologia Experimentalis et Applicata* 89, 47-55; 20- *IOBC/wprs Bulletin* 22, 7; 21- *Ecology* 84, 91-107; 22- *Biological Control* 29, 260-269; 23- *Biological Control* 28, 265-270; *Environmental Entomology* 34, 410-416; 24- *Environmental Entomology* 33, 356-361.

Table 3. Negative impacts of *H. axyridis* on plants.

Plant attacked	Country or States	References
1 Apples	Minnesota, USA	Hutchison <i>et al.</i> 2003
2	Minnesota, USA	Koch <i>et al.</i> 2004
3	Ohio, USA	Kovach 2004
4 Grapes	North Central USA	Ratcliff 2002
5	Ohio, USA	Williams <i>et al.</i> 2002
6	Ontario, Canada; Northern USA	Ejbich 2003
7	Minnesota, USA	Hutchison <i>et al.</i> 2003
8	Minnesota, USA	Koch <i>et al.</i> 2004
9	Ohio, USA	Kovach 2004
10	Ontario, Canada; Ohio, USA	Pickering <i>et al.</i> 2004
11 Peaches	Ohio, USA	Kovach 2004
12 Plums	Québec, Canada	M. Roy pers. comm.
13 Pumpkins	Minnesota, USA	Koch <i>et al.</i> 2004
14 Raspberries	Minnesota, USA	Hutchison <i>et al.</i> 2003
15	Minnesota, USA	Koch <i>et al.</i> 2004

Note: 1- *Minnesota IPM vegetable Newsletter* 5; 2- *Journal of Economic Entomology* 97, 539-544; 3- *American Entomologist* 50, 159-161; 4- USDA CSREES Regional Integrated Pest Management Program and the Pest Management Centers, 1-2. 5- *Arthropod Management Tests* 27, L14. 6- *Wine Spectator* 15 May, 16; 7- same as 1; 8- same as 2; 8- same as 3; 10- *American Journal of Enology and Viticulture* 55, 153-159; 11- same as 3; 13- same as 2; 14- same as 1; 15- same as 2.

***Harmonia axyridis* as a food source**

In ecosystems, high-order natural enemies may benefit from the establishment of a new introduced species if this new abundant biomass can be exploited. However, *H. axyridis* appears to have few natural enemies in habitats where it has been introduced. Although several parasitoids have been reported to attack *H. axyridis*, none have been considered effective in managing populations (Firlej *et al.* 2005, Katsoyannos and Aliniaze 1998). Disease organisms such as the entomopathogenic fungi *Beauveria bassiana* (Balsamo) seem not to infect *H. axyridis* (Cottrell and Shapiro-Ilan 2003). Observations—in the palearctic zone indicated that eight bird species effectively prey on this Coccinellid species, but they exert limited control (Netshayev and Kuznetsov 1973 in Hodek and Honěk 1996). No experiments have been carried out in North America to evaluate mortality caused by birds.

These studies raised two points. First, *H. axyridis* seems relatively enemy-free in the invaded countries and, second, higher-order enemy species are unable to successfully exploit this lady beetle as a food source.

***Harmonia axyridis* as a public nuisance**

In eastern North America during the mid 1990's, we began receiving reports from homeowners that ladybugs were infesting their houses. At first, it was difficult to believe that people were complaining about a few lady beetles in their homes (don't they realize that they are beneficial ?) but when millions were observed in their houses, we knew we had a problem. In the fall, adults lady beetles enter houses through cracks and crevices. Homeowners reported that during the swarming period (in the fall), they cannot leave the house without being covered with beetles that frequently bite (Huelsman and Kovach 2004). When present in large numbers, *H. axyridis* aggravate homeowner by making their way into food and drinks, and disrupting activities such as sleeping and reading. In addition when *H. axyridis* is

disturbed, they reflex bleed a yellow-orange, foul-smelling liquid that stains many surfaces and clothing (Huelsman and Kovach, 2004). Also they can be a nuisance in hospitals and testing facilities of pharmaceutical companies where there is a zero tolerance for biocontaminants (Nalepa *et al.* 2005).

Harmonia axyridis is becoming a nuisance in Europe where first observations in houses were recorded in Belgium during autumn 2004 (San Martin *et al.*, 2005). Usually *H. axyridis* invades the same sites each year, which lowers the property value of the targeted houses. Because of this overwintering behaviour, *H. axyridis* is now considered a public nuisance (Table 4).

Harmonia axyridis can induce allergic reactions in some people. Yarbrough *et al.* (1999) were the first to document an allergy caused by a member of the Coccinellid family or with an insect used as a biocontrol agent. In an Ohio survey, up to 26% of homeowners reported some allergic reaction when they were living with large infestations of *H. axyridis* (Hueslman and Kovach 2004). Observations of *H. axyridis* invading beehives were also reported (Table 4).

What have we learned from our experience with *H. axyridis*?

In classical biological control programs, specialist and generalist biocontrol agents are compared according to their efficacy and innocuity. It is now recognized that generalist biocontrol agents will have low success in biological control program with high probability to generate nontarget effects (Kimberling 2004; van Lenteren *et al.* 2003). As illustrated by the generalist biocontrol agent *H. axyridis*, nontarget impacts could be surprising and the situation can quickly become out of control. It highlights also the fact that insects have no frontiers (the beetle reached relatively northern latitudes of Canada in just a few years) and that agents often spread to distant areas where they are unwanted (Simberloff *et al.* 2005). It is impossible to evaluate the overall biological and economic impact of this lady beetle, now and in the future. This case could be however a key tool to identify characteristics to be

evaluated in cost-benefits analyses and risk assessment procedures that have to be done before introduction of new biocontrol agents (Colautti *et al.* 2006; Perrings *et al.* 2005; Simberloff 2005).

The final word

Before the arrival of *H. axyridis* in North America, natural and agricultural systems suffered from the arrival of at least three other exotic lady beetles (*Coccinella septempunctata* L., *Propylea quatuordecimpunctata* L., *Hippodamia variegata* Goeze). Composition of the guilds has been impacted by these successive waves of immigrants, but was only of concern to entomologists and ecologists. As pointed out by Elliott *et al.* (1996) for the release of *C. septempunctata*, it is essential to weigh the potential benefits of the release of a polyphagous predator such as *C. septempunctata* or *H. axyridis*. The story of *H. axyridis* should serve as a wake up call to all biocontrol specialists and should constitute a lesson for researchers, civil servants and all persons involved in the programs. This was an example of a human action with huge economic and ethical consequences. Learning from this experience may allow us to select and adopt a legislative framework for the future.

Table 4. Negative impacts of *H. axyridis* on humans.

Action	Negative Impact	Country or states	References
1 overwintering in beehives	nuisance to beekeepers	Delaware, USA	Caron 1996
2 overwintering in boxes at railroad crossing	prevent upward movement of the signal alarm	Florida, USA	Mizell 2002
3 overwintering in houses	allergic rhinoconjunctivitis	USA	Yarbrough <i>et al.</i> 1999
4	bite	Ohio, USA	Huelsman <i>et al.</i> 2001
5		Ohio, USA	Kovach 2004
6	nuisance	Georgia, USA	Tedders and Schaeffer 1994
7		North Carolina, Virginia, USA	Kidd and Nalepa 1995
8		North Carolina, Virginia, USA	Nalepa <i>et al.</i> 1996
9		Oregon, USA	LaMana and Miller 1996
10		Ontario, Canada	Hagley 1999
11		Belgium	Adriaens <i>et al.</i> 2003
12		Pennsylvania, USA	Riddick <i>et al.</i> 2000; 2004
13		Belgium	San Martin <i>et al.</i> 2005
14		Quebec, Canada	Labrie <i>et al.</i> unpublished data
15	odor	Ohio, USA	Huelsman <i>et al.</i> 2001
16	stained on walls	Ohio, USA	Huelsman <i>et al.</i> 2001
17		Belgium	San Martin <i>et al.</i> 2005

Note: 1- *American Bee Journal* 136, 728-729; 2- Florida Entomological Society, 85 Annual Meeting July 28-31 Clearwater Beach Florida, USA; 3- *The Journal of Allergy and Clinical Immunology* 104, 704-705; 4- <http://ipm.osu.edu/ladylicup.htm>; 5- *American Entomologist* 50, 159-161; 6- *Entomological News* 105, 228-243; 7- *Proceedings of the Entomological Society of Washington* 97, 729-731; 8- *Annals of the Entomological Society of America* 89, 681-685; 9- *Biological Control* 6, 232-237; 10- *Publication 208 Agriculture and Agri-Food Canada and Ontario Ministry of Agriculture, Food and Rural Affairs*; 11- *Belgium Journal of Zoology* 133, 195-196; 12- *Annals of the Entomological Society of America* 93, 1314-1321; *Journal of Entomological Science* 39, 373-386; 13- *Insectes* 136, 7-11; 15- same as 4; 16- same as 4; 17- same as 13.

ACKNOWLEDGEMENTS

We thank Douglas J. Parker (Canadian Food Inspection Agency, Ottawa) and Christie Bahlai (University of Guelph) for commenting the manuscript.

REFERENCES

- Adriaens, T., Branquart, E. and Maes, D. (2003) The multicolored asian ladybird *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), a threat for native aphid predators in Belgium? *Belgium Journal of Zoology*, **133**, 195-196.
- Chapin, J.B. and Brou, V.A. (1991) *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, **93**, 630-635.
- Coderre, D., Lucas, E. and Gagné, I. (1995) The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) in Canada. *The Canadian Entomologist*, **127**, 609-611.
- Colautti, R.I., Bailey, S.A., van Overdijk, C.D.A., Amundsen, K. and MacIsaac, H.J. (2006) Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions*, **8**, 45-59.
- Cottrell, T.E. and Shapiro-Ilan, D.I. (2003) Susceptibility of a native and an exotic lady beetle (Coleoptera: Coccinellidae) to *Beauveria bassiana*. *Journal of Invertebrate Pathology*, **84**, 137-144.
- de Almeida, L.M. and da Silva, V.B. (2002) Primeiro registro de *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae): um coccinelideo originario da regio Paleartica. *Revista brasileira Zoologica*, **19**, 941-944.
- Dixon, A.F.G. (2000) Insect predator-prey dynamics : ladybird beetles and biological control. Cambridge University Press, Cambridge.
- Elliott, N., Keickhefer, R. and Kauffman, W. (1996) Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia*, **105**, 537-544.
- Ejbich, K. (2003) Producers in Ontario and northern U.S. bugged by bad odors in

- wine. *Wine Spectator*, **15** May, 16.
- Firlej, A., Boivin, G., Lucas, É. and Coderre, D. (2005) First report of *Harmonia axyridis* Pallas being attacked by *Dinocampus coccinellae* Schrank in Canada. *Biological Invasions*, **7**, 553-556.
- Gordon, R.D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of New York Entomological Society*, **93**, 1-912.
- Hodek, I. and Honěk, A. (1996) Ecology of Coccinellidae. Kluwer Academic Publishers. Dordrecht/Boston/London.
- Huelsman, M.F. and Kovach, J. (2004) Behavior and treatment of the multicolored Asian lady beetle (*Harmonia axyridis*) in the urban environment. *American Entomologist*, **50**, 163-164.
- Iablokoff-Khnzorian, S.M. (1982). Les coccinelles, Coléoptères-Coccinellidae. Société Nouvelle des Éditions Boubée, Paris.
- Katsoyannos, P. and Aliniaze, M.T. (1998) First record of *Strongygaster triangulifera* (Loew) (Diptera : Tachinidae) as a parasitoid of *Harmonia axyridis* (Pallas) (Coleoptera : Coccinellidae) in western North America. *The Canadian Entomologist*, **130**, 905-906.
- Kimberling, D.N. (2004) Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. *Biological Invasions*, **6**, 301-318.
- Koch, R.L. (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science*, **3**, 1-16.
- Lucas, É. (2005) Intraguild predation among aphidophagous predators. *European Journal of Entomology*, **102**, 351-364.

- Majerus, M., Strawson, V. and Roy, H. The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. *Ecological Entomology*, **31**, 207-215.
- Nalepa, C.A., Kennedy, G.C. and Brownie, C. (2005) Role of visual contrast in the alighting behavior of *Harmonia axyridis* (Coleoptera: Coccinellidae) at overwintering sites. *Environmental Entomology*, **34**, 425-431.
- Perrings, C., Dehnen-Schmutz, K., Touza, J. and Williamson, M. (2005) How to manage biological invasions under globalization. *Trends in Ecology and Evolution*, **20**, 212-215.
- Pervez, A. and Omkar. (2006) Ecology and biological control application of multicoloured Asian ladybird, *Harmonia axyridis*: A review. *Biocontrol Science and Technology*, **16**, 111-128.
- Polis, G.A., Myers, C.A. and Holt, R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, **20**, 297-330.
- San Martin, G., Adriaens, T., Hautier, L. and Ottart, N. (2005) La coccinelle asiatique *Harmonia axyridis*. *Insectes*, **136**, 7-11.
- Simberloff, D. and Stiling, P. (1996) Risks of species introduced for biological control. *Biological conservation*, **78**, 185-192.
- Simberloff, D. (2005) The politics of assessing risk for biological invasions: the USA as a case study. *Trends in Ecology and Evolution*, **20**, 216-222.
- Simberloff, D., Parker, I.M. and Windle, P.N. (2005) Introduced species policy, management, and future research needs. *Frontiers of Ecology and Environment*, **3**, 12-20.
- Van Lenteren, J.C., Babendreier, D., Bigler, F., Burgio, G., Hokkanen, H.M.T.,

Kuske, S., Loomans, A.J.M. and Menzler-Hokkanen, I. (2003) Environmental risk assessment of exotic natural enemies used in inundative biological control. *BioControl*, **48**, 3-38.

Yarbrough, J.A., Armstrong, J.L., Blumberg, M.Z., Phillips, A.E., McGahee, E. and Dolen, W.K. (1999) Allergic rhinoconjunctivitis caused by *Harmonia axyridis* (Asian lady beetle, Japanese lady beetle, or lady bug). *The Journal of Allergy and Clinical Immunology*, **104**, 704-705.